The Chonaphini, a Biogeographically Significant Milliped Tribe in Eastern and Western North America (Polydesmida: Xystodesmidae)

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ABSTRACT—The Chonaphini, the only Nearctic xystodesmid tribe represented in both the eastern and western faunal regions, is the only tribe in the family in which the prefemoral process is typically more complex and of greater taxonomic utility than the acropodite. The latter structure varies from narrowly blade-like to acicular, and excepting *Montaphe paraphoena*, n.sp., lacks secondary projections. The prefemoral process, however, is often elaborate with secondary structures arising from the stem. Six genera, three monotypic, and twelve species comprise the tribe, with *Semionellus* Chamberlin and *S. placidus* (Wood) inhabiting four areas in the eastern United States from southeastern Minnesota to westcentral Virginia. The other taxa occur west of the Continental Divide from Montana to north-central California and Vancouver Island, Canada. *Chonaphe* Cook is represented by two new and two established species in the United States, *C. evexa* and *schizoterminalis*, and *C. remissa* Chamberlin and *armata* (Harger). *Chonaphe cygneia* and *patriotica*, both authored by Chamberlin, and *C. serratus* Loomis and Schmitt are placed in synonymy under *C. armata*. *Montaphe elrodi* (Chamberlin), the dominant xystodesmid from eastern Washington to western Montana, is projected to occur in the southern extremity of central British Columbia adjacent to Idaho and northeastern Washington. *Metaxycheir* Buckett and Gardner and *Tubaphe* Causey are monotypic, *M. prolata* Buckett and Gardner occurring in eastern Washington and the adjoining part of northern Idaho, and the subcylindrical *T. levii* Causey occurring in wet rainforests of the Olympic Mountains and the southwestern corner of Vancouver Island. *Selenocheir* n. gen., characterized by a short prefemoral process less than half as long as the acropodite, consists of three new species ranging from southwestern Oregon to the northern California coast and the northern Sierra Nevada Mountains. Modern descriptions and illustrations are presented for all tribal taxa along with keys to genera and to the species of *Chonaphe* and *Selenocheir*.

The milliped family Xystodesmidae, the dominant Nearctic polydesmoid family, occurs in three general regions of the continent: the eastern United States and southern Ontario and Quebec, Canada, east of the Central Plains; from southern Texas and New Mexico to El Salvador; and along the Pacific Coast west of the Sierra Nevada and Cascade Mountains from Los Angeles to southern Alaska, with an eastward extension into western Montana (Shelley 1987). The family is also well represented in east Asia—Japan, the Riu Kiu Archipelago, Korea, the vicinity of Vladivostok, Russia, and an unknown area in central China (Hoffman 1978, 1979). Tribal continuity exists between Meso-America and the eastern Nearctic, as the Rhysodesmini, the only Meso-American tribe, is represented in eastern North America by 9 genera and over 20 species. Similarly, the Orophini and Harpaphini are represented in both the western Nearctic and Asiatic regions. There

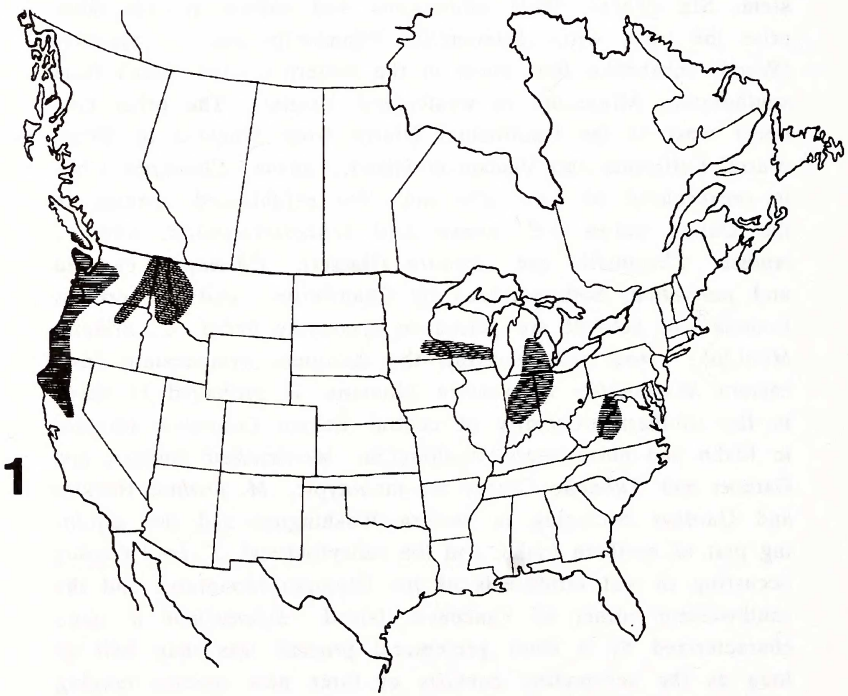


Fig. 1. Distribution of the Chonaphini. A smooth curve is drawn around range extremes in all directions. Though no records are available from the interior of British Columbia, the western interior region shows the projected occurrence of *M. elrodi* near the border with Idaho and northeastern Washington.

are no faunal linkages between the western Nearctic and Meso-America, and the Chonaphini is the only common tribe between the West and East.

The Chonaphini occurs primarily in the western United States and Vancouver Island, Canada (Fig. 1), where there are currently 5 genera and 11 nominal species (Shelley 1990, 1993*a*). West of the Columbia Plateau, *Tubaphe levii* Causey inhabits rainforests of the Olympic Mountains and Vancouver Island, and *Chonaphe armata* (Harger) and *C. remissa* Chamberlin occur sporadically in western Oregon and Washington, respectively (Shelley 1990, 1993*b*). In the western interior, the tribe is represented by *Montaphe elrodi* (Chamberlin), the dominant xystodesmid from eastern Washington to western Montana, *C. armata*, also occurring sporadically in western Montana, northern Idaho, and northeastern Oregon and Washington, and *Metaxycheir prolata* Buckett and Gardner, localized in Latah and Benewah counties, Idaho, and the adjacent eastern periphery of Whitman County, Washington (Buckett and Gardner 1969, Shelley 1990). I place three additional nominal species—*C. cygneia* and *patriotica*, both authored by Chamberlin, and *C. serratus* Loomis and Schmitt—in synonymy under *C. armata*. East of the Central Plains, the Chonaphini is represented by *Semionellus placidus* (Wood), which occurs primarily in three general areas: from southeastern Minnesota to eastern Wisconsin, from central Michigan to western Indiana, and from western Maryland to westcentral Virginia (Shelley 1990).

In addition to its biogeographic significance as a trans-Nearctic taxon, the Chonaphini is unique in that it reverses the basic anatomical pattern of the family. In other xystodesmid tribes, the gonopodal acropodite possesses most diagnostic features and is often elaborate, whereas the prefemoral process is variable but generally simple and with little taxonomic utility. In the Chonaphini, however, the acropodite is typically the simple structure, while the prefemoral process is usually larger and often elaborate, displaying flanges and other projections from its stem. The prefemoral process is thus the dominant feature of most chonaphine gonopods and exhibits most taxonomic characters. Indeed, the acropodite, usually a curved acicular to narrowly blade-like projection, is so thin and fragile in most species that it is easily broken during dissection, so care is needed to remove a gonopod with this structure intact.

With these basic attributes of the prefemoral process and acropodite, the Chonaphini seems at first to be a coherent assemblage whose study is comparatively straightforward, but there are undescribed forms that depart from this pattern, cannot be accommodated by other western

tribes, and appear to relate to known chonaphines. One species, *Montaphe paraphoena*, n. sp., occurring on the western periphery of the Columbia Plateau in central Washington, has a modified acropodite that expands distad and possesses a secondary projection. These features lend taxonomic utility to the acropodite and suggest that additional forms with expanded, modified acropodites, await discovery in central Washington. Because of similarities with *M. elrodi* in coloration and the curvature patterns of the telopodal elements, I provisionally assign this species to *Montaphe* instead of erecting a fifth monotypic genus, although this action necessitates a broad generic diagnosis resulting in a heterogeneous taxon. Furthermore, *Selenocheir*, n. gen., with three species in southern Oregon and northern/central California, is assigned to the Chonaphini even though it has a short prefemoral process that is less than half the length of the acropodite. The latter structure conforms to the tribal diagnosis in being narrowly blade-like to acicular, but differences in its orientation on the prefemur, in the broadness of its arc, and in the distal configuration again lend it taxonomic utility. This genus is more compatible with the Chonaphini than with any other western xystodesmid tribe, and traits of the prefemoral process and acropodite appear to represent plesiomorphic conditions that bridge anatomical gaps with the Harpaphini.

Thus the Chonaphini, which appears to be a homogeneous assemblage characterized by a narrow, unmodified acropodite and a long, elaborate prefemoral process, is really a highly variable ensemble with few consistent, unifying features; even the structures of the cyphopods and the configurations of the gonopodal apertures vary widely. *Tubaphe* and *Selenocheir* also lack a gonosternum, the coxae being attached by membrane only, and those taxa with a sclerotized band differ in the position of the sternal lobes. For example in *M. elrodi*, the sternum is short, resulting in narrowly segregated gonopods, and there are small lateral lobes subtending the coxae; in *M. paraphoena* the sternum is also short and the gonopods are narrowly separated, but there is an elongated medial lobe instead of two lateral ones. The Chonaphini, therefore, is not united by a few features shared by all included taxa but by a number of traits that are shared unevenly among the components such that only one higher category can be defined to encompass the scope of this variation. Efforts to divide the group and render it more homogeneous by splitting off dissimilar forms like *Tubaphe* and *Selenocheir*, which lack a gonosternum, or just the latter, which has the short prefemoral process, or *M. paraphoena*, with the medial sternal lobe and an expanded, modified acropodite, result in undefinable categories that cannot be contrasted with a recon-

stituted tribe Chonaphini. The chonaphine taxa therefore relate through differentially shared aspects of all the principal features; two forms that do not share one attribute share others, or relate through a third form with which they share still other features.

Separate taxonomic status for this assemblage was first proposed by Verhoeff (1941), who established the Chonaphinae as a subfamily in the "Leptodesmidae." Hoffman (1979) reduced the taxon to tribal status and listed *Chonaphe* Cook, *Montaphe* Chamberlin, *Semionellus* Chamberlin, and *Metaxycheir* Buckett and Gardner as component genera. He and I (Shelley 1990) placed *Tubaphe* Causey in the Harpaphini, an understandable misassignment because one gonopod of the holotype of *T. levii* Causey is lost, the other is broken, and the descriptive accounts and illustrations (Causey 1954*a*) do not begin to portray the taxonomically important features. I (Shelley 1990) proposed *Metaxycheir pacifica* for a chonaphine on Vancouver Island, British Columbia, that I subsequently (Shelley 1993*a*) had to place in synonymy under *T. levii* after recollecting the latter in the Olympic Mountains. Despite the unfortunate proposal of a synonym, my description and illustrations (Shelley 1990) make *T. levii* the only chonaphine taxon that has been characterized in accordance with modern standards. Most were proposed with terse accounts that merely validated the names, and one new genus and six new species await description. The purpose of this contribution, therefore, is to present modern descriptions and illustrations for all chonaphine taxa except *T. levii*, where such is provided in the account of *M. pacifica* (Shelley 1990). Acronyms of sources of preserved study material are as follows:

AMNH—American Museum of Natural History, New York, New York.
BYU—Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah.
CAS—California Academy of Science, San Francisco.
CMN—Canadian Museum of Nature, Ottawa, Ontario.
EIL—Zoology Department, Eastern Illinois University, Charleston.
FMNH—Field Museum of Natural History, Chicago, Illinois.
FSCA—Florida State Collection of Arthropods, Gainesville.
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MPM—Milwaukee Public Museum, Milwaukee, Wisconsin.
NCSM—North Carolina State Museum of Natural Sciences, Raleigh.
NMNH—National Museum of Natural History, Smithsonian Institution, Washington, D. C.

PMNH—Peabody Museum of Natural History, Yale University, New Haven, Connecticut.
RBCM—Royal British Columbia Museum, Victoria, British Columbia, Canada.
ROM—Royal Ontario Museum, Toronto, Ontario, Canada.
SDMNH—San Diego Museum of Natural History, San Diego, California.
TMM—Texas Memorial Museum, University of Texas, Austin.
UBC—Zoology Department, University of British Columbia, Vancouver, British Columbia, Canada.
UCD—Bohart Entomological Museum, University of California at Davis.
UMN—Entomology Department, University of Minnesota, St. Paul.
UWBM—Thomas Burke Washington State Museum, University of Washington, Seattle.
UWY—University of Wyoming Insect Museum, Laramie.
VMNH—Virginia Museum of Natural History, Martinsville.
WAS—Private collection of William A. Shear, Hampden-Sydney, Virginia.
WSU—James Entomological Museum, Washington State University, Pullman.
WU—Biology Department, Willamette University, Salem, Oregon.

LITERATURE REVIEW

The subfamily Chonaphinae was proposed by Verhoeff (1941) for *Chonaphe*, which was erected by Cook (1904) for *Polydesmus armatus*. This species was one of four myriapods that Harger (1872) described from an unspecified site along the John Day River, Oregon, which I (Shelley 1993*b*) inferred was near Canyon City, Grant County, on the western slope of the Blue Mountains. The third xystodesmid to be named from western North America, after *P.* (*Leptodesmus*) *haydenianus* Wood (1864), now in *Harpaphe*, and *P. dissectus* Wood (1867), now in *Motyxia*, *C. armata* is also the second oldest chonaphine species behind *P.* (*L.*) *placidus*, described by Wood (1864) from an unspecified site in Michigan. Immediately following the latter's description, Wood (1864) proposed the synonym, "*P.* (*L.*) *floridus* var.?," and Wood (1865) repeated the accounts of both species, providing a gonopod illustration of the former.

Sixteen years after Harger's work, Bollman (1888) recorded *L. placidus* from Boswell, Benton County, Indiana. In a listing of North American myriapods, Bollman (1893) included *L. armatus* and

placidus, placed *P. floridus* var.? in synonymy under the latter, and described *L. borealis* from Winona, Winona County, Minnesota. Kenyon (1893*a*, *b*) reported *L. floridus*, misspelled as "*floriaius*" in the first work, from four towns in Nebraska, as did Gunthorp (1913) from Jefferson County, Kansas, which Cragin (1885) previously recorded as *P. floridus*. Because these sites are well removed from the range of *S. placidus*, Shelley (1989) concluded that the usages refer to eurymerodesmids and placed the names in synonymy under species of *Eurymerodesmus*.

The first reference to a chonaphine in the present century was by Carl (1903), who redescribed *L. placidus*. Cook (1904) erected *Chonaphe* and assigned the new combination, *C. armata*, to a specimen from an unspecified site in Washington. Chamberlin (1911) recorded *L. armatus* from Madison, Washington, probably a misspelling of Madson, Whitman County, a now non-existent community not far from Viola, Latah County, Idaho. Chamberlin (1913) described *L.* (*C.*) *elrodi* from Flathead Lake, Montana, and in a statement in an introductory paragraph of a paper on an unrelated polydesmoid, he (Chamberlin 1920) proposed *Semionellus* and designated *L. placidus* as the type species. Apparently unaware of this action, Williams and Hefner (1928) recorded *L. placidus* from Allen, Hardin, Wood, and Seneca counties, Ohio. Attems (1938) published anatomical treatments and illustrations of *C. armata*, "*Trichomorpha*" *placida*, and "*Amphelictogon*" *elrodi*, but his (Attems 1931) account and illustrations of *C. armata* from a farm near Olympia, Thurston County, Washington, clearly refer to *C. remissa*, described by Chamberlin (1949). Consequently, his 1938 treatment of *C. armata* is really of both congeners.

After Verhoeff (1941) erected the Chonaphinae, Chamberlin (1946) described *C. michigana*, from Midland County, Michigan, and two years later (Chamberlin 1948), transferred this species to *Semionellus*. In the latter paper, he also described and illustrated *S. tertius*, from Kerrville, Kerr County, Texas, and in the previous year, he (Chamberlin 1947) recorded *S. placidus* from Garrett County, Maryland. Chamberlin (1949) transferred *L.* (*C.*) *elrodi* into the new genus, *Montaphe*, and described three new species of *Chonaphe*: *C. cygneia*, from White Swan, Yakima County, Washington; *C. patriotica*, from Fourth of July Canyon, Kootenai County, Idaho; and *C. remissa*, from Puyallup, Pierce County, Washington. Chamberlin (1951) recorded *S. placidus* from Fort Benning, Chattahoochee/Muscogee counties, Georgia, a misidentification of the introduced paradoxosomatid *Oxidus gracilis* (Koch), as noted by Shelley (1990). Causey (1952) recorded *Trichomorpha placida* from Dane and Milwaukee counties, Wisconsin, and a cave in

Union County, Illinois. Causey (1954*a*) erected *Tubaphe* for *T. levii*, from the Olympic rain forest, Jefferson County, Washington, and (Causey 1954*b*) recorded *M. elrodi* from Evans, Stevens County, Washington. Johnson (1954) included *S. placidus* among his list of Michigan millipeds but gave no specific localities. Chamberlin and Hoffman (1958) listed all species recognized at that time, added New York and Virginia to the range of *S. placidus*, placed *L. borealis* and *S. michigana* in synonymy, and transferred *S. tertius* into the chelodesmid genus *Aphelidesmus*, where it clearly belongs. Its purported occurrence in Texas can only reflect a labelling error, as the genus otherwise occurs from Costa Rica southward (Hoffman 1979).

Little has appeared on the Chonaphini in recent years. Hoffman (1969) noted that *Semionellus* is monotypic, related to *Chonaphe* and *Montaphe*, and cited its range as being from Minnesota to Illinois and Ohio, with isolated populations in western Maryland, the adjacent part of West Virginia, and the Virginia Blue Ridge. Buckett and Gardner (1969) erected *Metaxycheir* for *M. prolata*, occurring near Moscow, Latah County, Idaho, which they erroneously recorded as Nez Perce County. They correctly related *Metaxycheir* to *Chonaphe*, but apparently unaware of Verhoeff's subfamily, placed these genera, along with *Harpaphe* Cook and *Hybaphe* Cook, in the Orophinae, erected by Hoffman (1964) to accommodate *Orophe* Chamberlin and *Pamelaphe* Hoffman. This heterogeneous taxon was disassembled by Hoffman (1979), who transferred *Harpaphe* and *Hybaphe* to the new tribe Harpaphini and reduced the Chonaphinae and Orophinae to tribal status. Loomis and Schmitt (1971) described the final nominal species, *C. serratus*, from Sanders and Lake counties, Montana, alluded to the occurrence of *C. armata* along Puget Sound, Washington, where the only congener is *C. remissa*, and reported numerous new records of *M. elrodi* from Lake, Missoula, and Sanders counties, Montana, and Idaho County, Idaho.

The final relevant works concern Canada. Kevan (1983) listed all the taxa as potential Canadian inhabitants, and Shelley (1990) described *Metaxycheir pacifica* from Vancouver Island and summarized the distribution of the tribe and its generic and specific composition, omitting *Tubaphe* and *T. levii*. Shelley (1993*a*) synonymized *M. pacifica* under *T. levii* after recollecting the latter in the Olympic Mountains.

Thus, at this writing, five genera and nine species comprise the Chonaphini. They are listed chronologically below along with type localities and other reported occurrences.

Chonaphe Cook, 1904.

C. armata (Harger 1872). Vicinity of Canyon City, Grant County, Oregon, as deduced by Shelley (1993*b*). Also recorded from Washington in general (Cook 1904, Attems 1938); and the Puget Sound area (Loomis and Schmitt 1971); Oregon (Attems 1938, Chamberlin and Hoffman 1958); Idaho (Attems 1938); Madson (misspelled as Madison), Whitman County, Washington (Chamberlin 1911); near Olympia, Thurston County, Washington (Attems 1931); and Benton, Clackamas, and Multnomah counties, Oregon; King, Chelan, Kittitas, and Stevens counties, Washington; Latah and Clearwater counties, Idaho; and Lincoln and Missoula counties, Montana (Shelley 1990).

C. cygneia Chamberlin 1949. White Swan, Yakima County, Washington.

C. patriotica Chamberlin 1949. Fourth of July Canyon, Kootenai County, Idaho.

C. remissa Chamberlin 1949. Puyallup, Pierce County, Washington.

C. serratus Loomis and Schmitt 1971. 1.0 mi (1.6 km) west of Noxon, Sanders County, Montana. Also recorded from 4.0 mi (6.4 km) west of Noxon and 2.0 mi (3.2 km) north of Yellow Bay, Lake County, Montana.

Semionellus Chamberlin, 1920.

S. placidus (Wood 1864). Michigan without further specification. Also recorded from Minnesota, Illinois, and Ohio (Hoffman 1969); Michigan (Wood 1865, Attems 1938, Johnson 1954); New York and Virginia (Chamberlin and Hoffman 1958); western Maryland and adjacent West Virginia (Hoffman 1969); the Virginia Blue Ridge (Hoffman 1969); Winona, Winona County, Minnesota (Bollman 1893); Dane and Milwaukee counties, Wisconsin (Causey 1952); Union County, Illinois (Causey 1952); Midland County, Michigan (Chamberlin 1946); Boswell, Benton County, Indiana (Bollman 1888); and Allen, Hardin, Wood, and Seneca counties, Ohio (Williams and Hefner 1928).

Montaphe Chamberlin, 1949.

M. elrodi (Chamberlin 1913). Flathead Lake, Lake/Flathead counties, Montana. Also recorded from Evans, Stevens County, Washington (Causey 1954*b*, Shelley 1990); Spokane and Whitman counties, Washington (Shelley 1990); Lowell, Idaho County, Idaho (Shelley 1990) and 3.1 mi (5.0 km) west of Surveyor Creek, Idaho County (Loomis and Schmitt 1971); Clearwater and Shoshone counties, Idaho (Shelley 1990); and numerous localities in Lake, Missoula, and Sanders counties, Montana (Loomis and Schmitt 1971).

Tubaphe Causey, 1954*a*.

T. levii Causey (= *Metaxycheir pacifica* Shelley). Graves Creek

Campground, Olympic National Park, Jefferson County, Washington. Also known from Port Renfrew and seven other sites along the Pacific Coast in the southwestern corner of Vancouver Island, British Columbia, Canada (Shelley 1990).

Metaxycheir Buckett and Gardner, 1969.

M. prolata Buckett and Gardner. 7 mi (11.2 km) northeast of Moscow, Latah County, Idaho. Also known from Laird Park, cited as Laird "Peak," 3.0 mi (4.8 km) southeast of Harvard, Latah County (Shelley 1990).

ANATOMY AND TAXONOMIC CHARACTERS

Color—The overall "rust" colored appearance distinguishes species of *Montaphe* from sympatric xystodesmids of all tribes—Orophini, Harpaphini, and Chonaphini—and I have even noticed a tinge of this pigmentation in dried specimens that have been out of alcohol for years. I characterize the color as "rust" because it is a muted or dampened red, as if mixed with a touch of brown, as opposed to the bright red of Appalachian species of *Sigmoria* (Shelley and Whitehead 1986). The rust color seems characteristic of the genus, as the pigment was clearly evident in the type series of *M. paraphoena* after 1 1/2 years in preservative. The color is actually restricted to the paranota and concolorous bands along the caudal margins of each metatergite, but the latter are so broad as to cover most of the metazona and dominate the organism. Although one notices the dark gray to black base color, the rust pigmentation overwhelms one's senses and identifies the milliped as a representative of *Montaphe*.

The red banded pattern of *Semionellus placidus* is less distinctive than the color of *Montaphe* spp., but in its range, *S. placidus* is about the only xystodesmid displaying this color. An occasional specimen of *Sigmoria* (*Rudiloria*) spp. may show reddish stripes, but this pattern is exhibited primarily by congeners to the south in the Carolinas, Tennessee, and Georgia (Shelley and Whitehead 1986). Yellow is the dominant color in the forms of *Sigmoria*, *Apheloria*, and *Brachoria* that are sympatric with *S. placidus*.

Body Form and Somatic Features—*Tubaphe levii* and *S. placidus* are readily identified by their general body forms. As noted by Shelley (1990), the unmistakable, nearly julidan appearance of the caudal 2/3 of its body, caused by the absence of paranota caudal to segment 4 (Fig. 45), instantly distinguishes *T. levii* from sympatric specimens of *Harpaphe h. haydeniana*. Though less distinctive, the generally subcylindrical body form, caused by reduced and declined paranota, also distinguishes *S. placidus* from the much broader and more robust

sympatric representatives of the Apheloriini and Rhysodesmini. Combining body form with color pattern allows one to unfailingly recognize *S. placidus* in the field.

Aside from the size and degree of decline of the paranota, there are few noteworthy aspects of the somatic details. The epiproct of *T. levii* displays a narrow constriction (see Causey 1954*a*, fig. 2), whereas those of the other taxa are smoothly subtriangular. Low lateral ridges subtend the anterior coxae, and the glaborous pregonopodal sterna, depressed on segment 6 and the caudal half of segment 5 to accommodate the gonopodal telopodites, generally lack modifications aside from long, diverging projections on the 4th sternite of *S. placidus* (Fig. 27). The postgonopodal sterna also are glabrous and unmodified, with only shallow transverse grooves between the leg pairs and gently curved caudal margins. The pregonopodal coxae of *Metaxycheir prolata* are swollen with slight anteriorly directed lobes but are unmodified in other species. Prefemoral spines are present in all species, but only on postgonopodal legs and often only in the caudal half of the body.

Aperture—The aperture in the Chonaphini usually extends caudad to at least a small degree in the midline. The only exceptions are *T. levii* and *Chonaphe evexa*, which resemble other northwestern xystodesmids in lacking even a trace of a caudal extension (Figs. 15, 46). This feature of the aperture is particularly noticeable in *C. armata* and *S. placidus* (Figs. 2, 28), which have long, broad extensions, and is another trait that distinguishes the latter from sympatric representatives of other eastern tribes. Within these extensions is a sclerotized ledge or shelf that I believe represents the sternum between the 9th legs. Thus, it is really only the elevated caudal margin that extends or "peels" caudad, analogous to "peeling" the backing off a gummed label; the opening itself is ovoid to elliptical. However, in *C. armata* and *S. placidus*, the extensions are so obvious as to appear a functional part of the opening even though they are not.

Gonopods—As stated previously, the Chonaphini is unique in that the prefemoral processes are highly variable and possess most taxonomically important features, whereas the acropodites are simple and with little taxonomic utility, as opposed to the reverse in all other xystodesmid tribes. All genera and most species can be diagnosed from aspects of the prefemoral process, which is the dominant gonopodal feature, overshadowing the acropodite in most forms. The arrangements of the telopodal elements relative to each other are also important, the prefemoral process and acropodite being subparallel in *Semionellus* and *Montaphe*, and not parallel in the other genera. It is this shared

parallel arrangement coupled with the shared rust color that support placement of *paraphoena* in *Montaphe* along with *elrodi*.

Prefemoral Process—There are three basic types of prefemoral processes: the short projections of *Selenocheir* that are less than half as long as the acropodites (Figs. 54–55, 60–61, 65–66); long ones, as long or longer than the acropodite, that are narrowly blade-like to subacicular (Figs. 35–38, 47–48, 52–53); and long ones that are expanded, broad, and laminate (Figs. 3–7, 10–13, 16–19, 22–25, 30–31). The distally expanded, trifurcate projection of *Montaphe paraphoena* (Figs. 42–43), shorter than the acropodite, is an exception. The massive structures of *Chonaphe* and *Semionellus* are especially lamellate distad. In *Chonaphe*, the projection is upright and expands at about 1/3 length into a narrow shelf or ledge on the dorsal side. The outer margin of the ledge extends distad a short distance as a translucent shield; in *C. schizoterminalis* a distal angular flap on the stem of the prefemoral process overlaps the shield to form a tube; and in *C. remissa* the shield connects to the inturned lateral margin of the stem to form a continuous lamina that extends to the tip of the process. The distal part of the acropodite inserts onto this shield or through the tube and extends for varying lengths, emerging from behind the shield and becoming visible in medial view in *C. armata* and *evexa* (Fig. 5), while being obscured by the continuation of the shield and its linkage with the inturned lateral margin in *C. remissa* (Fig. 11). Distal to the shelf, there is the flap of *C. schizoterminalis* (Fig. 23), a low angular ridge in *C. evexa* (Fig. 18), and a thickened, convoluted projection in *C. armata* and *remissa* about halfway between the ledge and the tip (Figs. 5–6, 11–12). Taxonomically, the most important aspect of the prefemoral process of *Chonaphe* is the apical configuration, which is a modification of a basically subdivided structure. In *C. schizoterminalis*, the tip is deeply divided lateral to the midline into two apical projections, a narrow, lateral, dactyliform branch that is subequal in length to the larger, medial branch (Figs. 22–24). The process is apically entire in *C. evexa*, but the subterminal lateral margin turns inward for a short distance to form a narrowly rounded lobe, suggesting an apical division that has become subapical as the apical-medial margin has enlarged and expanded (Figs. 18–19). The impression that I receive from *C. armata* and *remissa* is of formerly divided apices that have rejoined, with the suture line still being evident in the latter, particularly when viewed in ventral perspective (Fig. 13). In both species, it is as if a previous division has disappeared, leaving a vertical, coaxial flap or sclerotized, marginally serrate lamella in *C. remissa* (Figs. 10–12), and an inturned, subacuminate, transverse medial corner in *C. armata*

(Figs. 4–6). Thus, although taxonomically important features occur on several parts of the prefemoral process, all four species of *Chonaphe* can be diagnosed solely from the apical configuration. It seems ironic that such significance can accrue to such a minute part of this massive structure.

Though large, expanded, and laminate, the prefemoral process of *Semionellus* (Figs. 30–31) has a different configuration from that of *Chonaphe*. Instead of being upright, it bends strongly, at about a right angle, near 1/3 length and exhibits cupulate flanges on the medial surface proximal and distal to this bend. There is no ledge or shield as in *Chonaphe*, but occasionally the acropodite extends through the concavity of the proximal flange. The margins of these flanges, particularly the proximal one, are highly irregular and sometimes jagged, with minute serrations, larger teeth, and in some individuals, a secondary proximal flange, also marginally irregular, arising from the basal lamella; the distal flange is further ornamented by a strong, distally directed spine from the caudal margin. The distal 1/3 of the prefemoral process expands to a subacuminate tip on the inner distal corner, but its principal characteristic is a dense pilosity that arises from the inner and apical margins and nearly obliterates the tip. There are two kinds of hairs—long, relatively straight ones arising marginally and submarginally, and short, curved ones that arise from an overhanging ledge on both the medial and lateral sides and extend at most only to the level of the first hairs. These distal hairs, apomorphic for *Semionellus*, are unique not only in the Chonaphini but also in the family Xystodemidae. I know of no other xystodesmid genus with hairs on either the prefemoral process or acropodite.

The other type of prefemoral process is the narrow projection, which is blade-like, at least basally, in *Montaphe elrodi* and *Metaxycheir*, and subacicular in *Tubaphe*. It curves generally bisinuately, lacks secondary structures in *Metaxycheir* (Figs. 52–53), and subtends a variable arc and possesses modifications in *Montaphe* and *Tubaphe* (Figs. 35–38, 47–48). The projection curves gently and displays minute apical barbules from the inner margin in *Tubaphe* (Figs. 47–48), the latter being shared with *Montaphe elrodi*, in which the barbs are strongly pronounced and extend proximad on the stem of the projection, though still clustered apically (Figs. 35–38). In *M. elrodi* the prefemoral process bends or curves dorsad near midlength, extending well beyond the acropodal curvature, excepting individuals in which the latter is distended (Fig. 38), and tapering smoothly and continuously to a subacuminate tip. The barbs are located distad, and proximal to the bend

is a large, variably cupulate projection from the medial surface with a variably serrate to strongly toothed and jagged distal margin. This structure further varies from a simple curved lamella, with a variably irregular distal margin, to one with two or three marginal lobes or folds, also with variably irregular distal margins.

Acropodite—Except for *Montaphe paraphoena*, chonaphine acropodites vary from narrowly blade-like to acicular, and though devoid of secondary structures, hold taxonomic utility in the general form of their curvatures and in their positions relative to the prefemoral process. Disposing first of *M. paraphoena*, its acropodite expands basally into a thickened, flange-like overhang on the outer medial surface and a strong lateral spine, which is positioned opposite the terminal expansion of the prefemoral process and is obscured by the latter in medial view (Figs. 42–43). Distally, the acropodite narrows somewhat and curls in a broad, open loop that encompasses the entire prefemoral process. By contrast in *M. elrodi*, the acropodite is typical for the tribe, being narrow basally and becoming still narrower and subacicular distad. It usually curls over the prefemoral process at the level of the latter's bend, but occasionally it is distended and lies subparallel to the prefemoral process (Figs. 35–38).

In both *Metaxycheir* and *Tubaphe*, the acropodite curves in the form of a broad, open loop, through essentially a single vertical plane in the latter and through more than one plane in the former. The structure is broader and blade-like in *Metaxycheir*, and its loop extends beyond the distalmost point of the prefemoral process (Figs. 52–53). In *Tubaphe* the acropodite is narrower, becoming acicular distad, and the prefemoral process extends either through the loop or below it (Figs. 47–48).

Chonaphe and *Semionellus* are the only two genera with truly acicular acropodites. In *Chonaphe* it curls around the prefemoral process, inserts onto the shelf, being obscured by the shield, and curves distad along the projection's medial face (Figs. 4–7, 10–13, 22–25). Occasionally the acropodite is displaced and curls above the shelf, thus being clearly visible for its entire length (Figs. 16–19). In *Semionellus* the structure bends strongly basally, is sublinear for most of its length, and curves broadly distad (Figs. 30–31). It typically lies below, and runs generally parallel to, the prefemoral process, but in a few males, it passes through the curvature of the proximal flange. In *Chonaphe*, the acropodite is somewhat coiled and passes through numerous vertical planes, whereas in *Semionellus*, the structure is nearly uniplanar.

Cyphopods—The female genitalia are positioned transversely in the cyphopodal aperture, which encircles the 2nd legs on segment 3;

the caudal margin of the aperture is strongly elevated above the metazonal surface and rises to a peak in the midline. The common valvular surface is visible *in situ*; the receptacle lies beneath the medial corners of the valves; and the operculum is closely appressed to their lateral surfaces. All these structures are hirsute, the receptacles having long hairs arising from the ventral margins and extending beyond the ventral margins of the valves. As the receptacles in other eastern tribes are glabrous, without even a trace of hairs, the hirsute ones enable females of *S. placidus* to be distinguished from sympatric females of other genera. In most chonaphines, the medial valvular margins project distinctly ventrad, thereby creating a central depression or cavity on the common, ventral surface (Figs. 8, 14, 20, 39, 49). *Semionellus* is an exception in that the ventral surface is flat, without a trace of a cavity or prolongation (Fig. 32), as is *C. schizoterminalis*, which has central valvular lobes (Fig. 26). In keeping with its structurally different gonopods, the cyphopods of *Selenocheir* have only slight suggestions of medial lobes and central impressions (Figs. 58, 63, 67). Likewise, the receptacle is alate in most species, being cupped below the medial corners of the valves, narrowing distinctly in the midline, and extending for varying lengths along the anterior and posterior sides of the valves. For the most part, the operculum is relatively large, a distinct sclerite lateral to the valves, instead of an indistinct structure as in most xystodesmids.

Tribe Chonaphini Verhoeff

Chonaphinae Verhoeff, 1941:403.
Chonaphini: Hoffman, 1979:157. Shelley, 1990:2313–2315.

Components—*Chonaphe* Cook, 1904; *Semionellus* Chamberlin, 1920; *Montaphe* Chamberlin, 1949; *Tubaphe* Causey, 1954*a*; *Metaxycheir* Buckett and Gardner, 1969; *Selenocheir*, new genus.

Diagnosis—A tribe of moderate-size Xystodesminae with the following characteristics: gonopodal aperture with caudal margin elevated, ovoid or extending caudad to varying degrees between 9th legs, sternum between latter present as "shelf" in caudal extension; gonocoxae joined by membrane, with or without sclerotized sternal band, latter usually with lobes subtending coxae, occasionally with medial lobe; telopodal elements parallel or not parallel; prefemoral process variable, often elaborately ornamented, short and less than half as long as acropodite or as long or longer than latter, ranging from acicular to narrowly blade-like to expanded and laminate, usually with projections arising from stem or with shallow or deep apical

cleft; acropodite usually simple and unmodified, acicular to narrowly blade-like, either circumscribing variably broad arc, with or without abrupt distal curvature change, bending anteriad at right angle proximally and curving broadly distad, or looping around prefemoral process and inserting on shelf on latter; cyphopods oriented transversely in aperture, with or without prolongations of medial valvular corners and variable central cavities, receptacles alate or flattened, hirsute with variable numbers of long hairs arising primarily from ventral margins.

Distribution—Occurring in parts of western North America and the eastern United States east of the Central Plains from southeastern Minnesota to the Blue Ridge Province of northern Virginia. Mapping the available museum records reveals that the range is divided into 7 separate areas (Fig. 1): along the Pacific Coast in the southwestern corner of Vancouver Island, British Columbia; from the Olympic Peninsula of Washington to the northern coast of California and the central Sierra Nevada Mountains, extending eastward across the Cascade Mountains in Washington to the western fringe of the Columbia Plateau Physiographic Province; from northcentral Oregon and eastern Washington to western Montana and Idaho north of the Salmon River, probably extending just across the International Border into southern British Columbia between Rossland and Creston; from southeastern Minnesota to southeastern Wisconsin; from the central lower peninsula of Michigan through western Ohio to western Indiana; a single site in southeastern Ohio near the Ohio River; and from western Maryland through eastern West Virginia to the Blue Ridge Province of westcentral Virginia, terminating in Shenandoah National Park.

Remarks—The anatomical diversity in this diplopod assemblage presents formidable obstacles to formulating a tribal diagnosis, as several key features have exceptions. The gonopodal apertures are large and expanded caudad in all chonaphines except *C. evexa*, *T. levii*, and *Selenocheir sinuata*; *T. levii* and the species of *Selenocheir* are the only representatives lacking a sternal remnant; *Montaphe paraphoena* is the only chonaphine lacking an acicular to narrowly blade-like acropodite and the only one with the gonosternum lacking lateral lobes; the species of *Selenocheir* are the only ones with short prefemoral processes; and *Metaxycheir prolata* is the only component with a long prefemoral process that lacks modifications. To my knowledge the Chonaphini is the only xystodesmid tribe in which the presence or absence of a sternum is not constant, but the narrow aperture of *Tubaphe* is shared with *C. evexa* and *S. sinuata*; the caudally extended apertures of *S. arcuata* and *S. directa* are shared with other chonaphines; and the barbules on the prefemoral process of *T. levii* are shared with

Montaphe elrodi. After evaluating all the specimens cited herein, it is apparent that all these genera are related and comprise a distinct faunal assemblage despite the absence of a unifying anatomical feature. The closest such trait is the narrowly blade-like to acicular acropodite, the only exception being *Montaphe paraphoena*.

The previous range description (Shelley 1990) was published before field expeditions to Washington, Idaho, and Montana. The specimens collected on these trips plus additional museum samples reveal that the distribution in the western United States is not contiguous and that a separate "finger" extends southward along the Blue Mountains into Oregon from eastern Washington. Foremost among the new specimens are the syntypes of *P. armatus* at the PMNH (Shelley 1993*b*), and three additional samples from Grant and Umatilla counties, Oregon (WAS), which confirm the species in this range. An additional record of *S. placidus* from eastern Ohio, shown as a solitary spot in figures 1 and 69, suggests that the central and eastern areas of this species may eventually be connected.

Key to Genera of the Chonaphini, based primarily on adult males.

1. Prefemoral process short, less than half as long as acropodite (Figs. 54–55, 60–61, 65–66); Jackson and Curry counties, Oregon, to Mendocino and El Dorado counties, California .... *Selenocheir*, new genus

   Prefemoral process longer, nearly as long as to longer than acropodite 2

2. Prefemoral process generally long and slender, acicular or blade-like, expanding only distad if at all, with or without variable processes 3

   Prefemoral process broadly expanded and laminate throughout length 5

3. Prefemoral process blade-like and unadorned, without projections, (Figs. 52–53); Latah and Benewah counties, Idaho .... *Metaxycheir* Buckett and Gardner

   Prefemoral process either with variably long barbules or distally expanded 4

4. Paranota variably broad and distinct throughout body; gonosternum present (Figs. 34, 41); Douglas County, Washington, to Lake County, Montana ..... *Montaphe* Chamberlin

   Paranota present on segments 1-5 only, remaining segments appearing nearly julidan, with at most only ozopore swellings (Fig. 45); gonosternum absent, coxae connected by membrane only; Vancouver Island, British Columbia, to

Jefferson County, Washington ..... *Tubaphe* Causey

5. Prefemoral process upright, without distal hairs; distal part of acropodite inserting onto narrow shielded ledge on prefemoral process (Fig. 47); King and Chelan counties, Washington, to Grant and Coos counties, Oregon, and Missoula County, Montana ..... *Chonaphe* Cook

Prefemoral process bent abruptly dorsad at 1/3 length, with dense distal hairs on inner and apical margins, without ledge; acropodite usually lying parallel to prefemoral process (Figs. 30–31); southeastern Minnesota to westcentral Virginia ..... *Semionellus* Chamberlin

Genus *Chonaphe* Cook

Chonaphe Cook, 1904:56. Attems, 1931:65; 1938:155–156. Chamberlin and Hoffman, 1958:27. Jeekel, 1971:253. Hoffman, 1979:157. Kevan, 1983:2968.

Type species—Polydesmus armatus Harger, 1872, by original designation.

Diagnosis—Paranota present and variably distinct on all segments; epiproct without constriction; gonocoxae widely segregated by narrow sternal band, latter with lateral lobes; telopodal elements not parallel, arising proximad on prefemur; prefemoral process long, expanded and laminate, elaborately ornamented, with shielded ledge or shelf near midlength on dorsal surface; acropodite acicular, passing through numerous vertical planes, looping around prefemoral process and curling onto shelf; cyphopod valves with medial corners usually prolonged ventrad, subtending central cavity.

Description—A genus of moderately large to large chonaphine Xystodesminae with the following characteristics:

Body composed of head and 20 segments in both sexes, essentially parallel sided, tapering at both ends.

Head of normal appearance, smooth, polished. Epicranial suture faint or distinct, terminating above interantennal region. Antennae relatively short and broad, becoming progressively more hirsute distad, with 4 conical sensory cones on ultimate article, no other sensory structures apparent. Genae not margined laterally, with faint or distinct central impressions, ends narrowly rounded and extending just beyond adjacent cranial margins. Facial setae with epicranial, interantennal, frontal, genal, clypeal, and labral series present, with or without supraantennal and subantennal series.

Terga smooth, polished. Collum relatively broad, ends terminating above or at same level as those of following tergite. Paranota moderate-size to well developed, broadest on segments 1-5/6, moderately declined, angling ventrolaterad and interrupting or continuing slope of dorsum, anterior corners rounded throughout or blunt on segments 2–3, caudolateral corners variable, either blunt or with suggestion of tooth on anteriormost segments and round on remaining tergites, or squared on anteriormost segments, becoming blunt in midbody region and blunt caudal to midlength. Peritremata broad, distinct to moderately distinct, moderately to strongly elevated above paranotal surface; ozopores located caudal to midlength, opening laterad to sublaterad. Caudal segments normal for family.

Sides of metazonites variable, with or without variable grooves, impressions, or ridges above pregonopodal coxae. Strictures distinct. Gonapophyses moderately long and stout. Pregonopodal sterna glabrous; 4th unmodified or with variable lobes, medially coalesced or widely segregated; 5th sternum with flattened ridges or low, widely segregated projections between anterior (4th) legs and depression between 5th legs; 6th sternum with strong depression between both legs to accommodate stems of telopodites, 7th legs set slightly farther apart than 6th. Postgonopodal sterna glabrous, with broad, shallow, central impressions but otherwise without modifications, caudal margins smooth, gently curved. Coxae without projections; prefemora either without ventrodistal spines or with variably short spines on legs in caudal half of body; tarsal claws gently curved. Hypoproct broadly rounded, paraprocts with margins strongly thickened.

Gonopodal aperture generally ovoid, either extending caudad between 9th legs or terminating anterior to latter, with or without slight anteriolateral indentations, anterior margin and anterior halves of sides flush with metazonal surface, latter elevating caudad and continuing onto caudal margin, either descending in midline or continuing at level elevation. Gonopods *in situ* with telopodites extending anteriad from aperture and lying parallel to each other, overhanging 6th and caudal half of 5th sterna. Coxae variable in size, either with 2, or linear field of 4–8, macrosetae, well separated from each other by narrow sternal band, latter with short to moderate lobes subtending coxae. Telopodal elements not parallel, arising proximad on prefemur; latter moderately long and slender; prefemoral process large, arising from anteromedial or anterior margins, narrow basally, expanding greatly at 1/3 to 1/4 length into ledge or shelf on dorsal side, outer margin extending beyond latter to form translucent shield, stem of prefemoral process continuing distad with variably irregular margins, either with

thickened irregular, convoluted projection on dorsal side at 3/4 length or with angular ridge or flange, stem either broadly rounded apically and with inturned lateral subapical lobe, or deeply divided with narrow lateral and broad medial terminations of subequal length, or with suggestion of division and with lateral side either bent strongly dorsad and transversely to stem, or not bent and with laminate, coaxial projection on dorsal side, or expanding distad and leaning over stem. Acropodite acicular, arising on caudal or caudolateral sides of prefemur, looping around prefemoral process and curling onto shelf, apically acuminate. Prostatic groove arising in pit in prefemur, extending along medial face of latter onto acropodite, running generally along inner surface of loop to apical opening.

Cyphopodal aperture broad, encircling 2nd legs, sides and caudal margin elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely, common surface visible in aperture. Valves variable in size, subequal, lightly to moderately hirsute, medial corners extending ventrad into variable lobes, subtending central depressions. Receptacle small to moderately large, hirsute, or with variable numbers of hairs arising from ventral margins, either cupped around valves or flat and inconspicuous. Operculum relatively large, located laterad to valves, with numerous long hairs.

Distribution—Occurring in five segregated areas in the northwestern United States as follows: Coos County, Oregon; Grant and Umatilla counties, Oregon; Benton County, Oregon, to Mason and Chelan counties, Washington; and Stevens and Whitman counties, Washington, to Missoula County, Montana. This total area covers about 468 mi (753 km) in the east-west dimension and 351 mi (565 km) in the north-south, and encompasses parts of the Northern Rocky Mountains, Columbia Plateau, Sierra Cascade, and Pacific Border Physiographic Provinces.

Species—Four are known; more may occur in isolated pockets within the generic range.

Key to Species of *Chonaphe* (based on adult males)

1. Prefemoral process with broad, thickened, convoluted projection from dorsal surface distal to shelf (Figs. 5–6, 11–12) 2
   Prefemoral process with angular ridge or expanded flap on dorsal surface distal to shelf (Figs. 16, 18, 22–23) 3
2. Apical margin of prefemoral process with lateral side acuminate, bent abruptly dorsad, lying transverse to axis (Figs. 4–6); Stevens and Chelan to Yakima counties, Washington; Multnomah to Benton and Umatilla to Grant counties, Oregon; and Sanders County, Montana, to Kootenai and Idaho

counties, Idaho ..... *armata* (Harger)

Distal extremity of prefemoral process with coaxial, marginally serrate projection on dorsal surface (Figs. 10–12); King and Mason to Skamania counties, Washington ..... *remissa* Chamberlin

3. Apical margin of prefemoral process broadly rounded, entire, distolateral margin inturned dorsad, forming short subterminal lobe; ridge on anterior surface only slightly elevated above stem of projection, not laminate (Figs. 16–19); Coos County, Oregon ..... *evexa*, new species

Apical margin of prefemoral process gently curved, deeply divided, lateral side forming long, slender dactyliform projection, subequal in length to broader medial projection; ridge on anterior surface elevated and expanded into laminate flange or flap, overlaying shield (Figs. 22–25); Stevens County, Washington ..... *schizoterminalis*, new species

Chonaphe armata (Harger)

Figs. 2–8

Polydesmus armatus Harger, 1872:119–120. pl. II, fig. 8.

Leptodesmus armatus: Bollman, 1893:122. Chamberlin, 1911:264.

Chonaphe armata: Cook, 1904:56–57, pl. III, figs. 2a-c. Attems, 1938 (in part):156, fig. 177. Chamberlin, 1949:125. Chamberlin and Hoffman, 1958:27. Kevan, 1983:2968. Shelley, 1990:2314; 1993*b*:9–10, figs. 4-5.

Chonaphe cygneia Chamberlin, 1949:125, fig. 1. Chamberlin and Hoffman, 1958:27. Kevan, 1983:2968. NEW SYNONYMY.

Chonaphe patriotica Chamberlin, 1949:127, figs. 2–3. Chamberlin and Hoffman, 1958, 1958:27. Kevan, 1983:2968. NEW SYNONYMY.

Chonaphe serratus Loomis and Schmitt, 1971:111–112, figs. 1-2. NEW SYNONYMY.

Chonaphe serrata: Kevan, 1983:2968.

Type specimens—One male and two female syntypes (PMNH) collected by O. Harger and G. H. Collier in October 1871 from the vicinity of Canyon City, Grant County, Oregon.

Diagnosis—Dorsal surface of prefemoral process with broad, thickened, irregular projection distal to shelf; apical margin sublinear to gently indented, lateral half curving anteriad and lying transversely to axis, apically acuminate; shield not connecting with lateral margin.

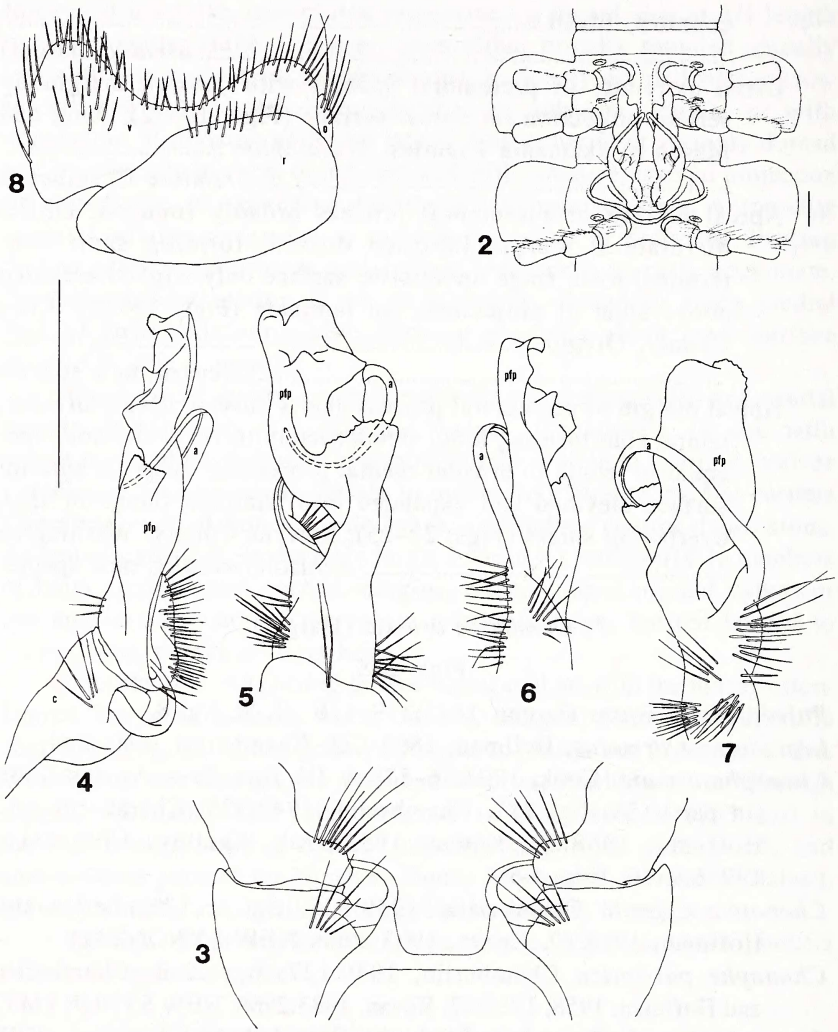


Fig. 2-8. *Chonaphe armata*. 2, gonopods *in situ*, ventral view of male from Latah County, Idaho. 3, gonocoxae and sternum, dorsal view of specimen from Chelan County, Washington. 4, left gonopod of male from Umatilla County, Oregon, medial view. 5, telopodite of the same, dorsal view. 6, the same, lateral view. 7, the same, ventral view. 8, left cyphopod of female from Latah County, Idaho, caudal view. a, acropodite; c, coxa; o, operculum; pfp, prefemoral process; r, receptacle; v, caudal valve. Scale line for Figure 2 = 1.00 mm; line for other Figures = 2.78 mm for 3, 2.00 mm for 4-7, 1.00 mm for 8.

Color in life—Metaterga black, without spots and usually without stripes, paranota white, cream-colored, yellow, or light reddish orange; collum without a stripe along anterior margin.

Male syntype—Length 23.3 mm, maximum width 4.3 mm, W/L ratio 18.5%, D/W ratio 65.1%. Body parallel sided for most of length, tapering at both ends.

Head capsule smooth, polished; epicranial suture shallow, indistinct, terminating above interantennal region. Width across genal apices 2.3 mm, interantennal isthmus 0.8 mm. Antennae appearing relatively short and broad, reaching back to caudal margin of 3rd tergite; relative lengths of antennomeres 2>3>6>4=5>1>7. Genae with moderately distinct central impressions, ends broadly rounded and extending slightly beyond adjacent cranial margins. Facial setae as follows: epicranial 1-1, interantennal absent, frontal 1-1, genal 3-3, clypeal about 8-8, labral about 12-12.

Collum broad, ends terminating at same level as those of adjacent tergite. Paranota well developed throughout body, broadest on segments 1-6, angling ventrolaterad but interrupting slope of dorsum, anterior corners rounded, caudolateral corners squared on segments 2–5, slightly acuminate on 6–8 and 11, blunt on 9–10 and 12–13, angling caudad on 14–17. Peritremata distinct, strongly elevated above paranotal surface; ozopores located caudal to midlength, opening sublaterad.

Sides of metazonites generally smooth, polished, with variable curved, shallow impressions. Pregonopodal sterna glabrous; 4th sternum unmodified; 5th sternum with two low, rounded, widely separated elevations between anterior (4th) legs and concave depression between 5th legs to accommodate apices of telopodites. Prefemora of legs on segments 11–18 with short but distinct, ventrodistal spines.

Gonopodal aperture extending caudad between 9th legs, 1.8-mm wide and 1.0-mm long at midpoint, without indentations, sides elevating into broadly rounded, caudolateral lobes, lower in midline. Gonopods *in situ* (Fig. 2, not this specimen) with telopodites situated in opposite sides of aperture, well separated from each other, extending anteriad in parallel arrangement over coxae of legs 6–7 (on segment 6), terminating over 5th legs and sternum of segment 5. Gonopod structure as follows (Figs. 3–7): Coxae of normal size and appearance, with linear fields of 4–6 macrosetae, well segregated by broad sternum, latter with moderate-size lateral lobes. Prefemur moderately long, with large prefemoral process arising from anteromedial surface, latter narrow basally and leaning slightly laterad, expanding at 1/3 length into ledge or shelf on dorsal side, outer margin extending beyond surface of ledge as translucent shield, stem of prefemoral process continuing distad

with irregular to lightly serrate edges, expanding again at 3/4 length into broad, thickened irregularly convoluted projection on dorsal side, distal extremity of stem thin and lamellate, apical margin gently concave, lateral side bent strongly dorsad, lying transversely to axis, apically acuminate, medial side not bent, apically rounded. Acropodite arising on caudolateral side of prefemur, angling anteromediad over ventral surface of prefemoral process, looping around medial surface of latter, and curling onto shelf, obscured by shield, curving distad along dorsal face of process to acuminate tip.

Female syntype—Body highly fragmented, length unmeasurable, maximum width 4.2 mm, D/W ratio 75.6%. Agreeing essentially with males in structural details except paranota more declined, giving appearance of slightly more vaulted body. Valves (Fig. 8) relatively large, moderately hirsute, with large medial lobes protruding through midline of aperture, subtending deep central depression. Receptacle large, lightly hirsute along ventral margin, cupped around valves, extending slightly more on caudal side than on anterior.

Variation—There is considerable variation in color. The pattern is generally bimaculate with colored paranota and uniformly black metaterga, but two males that I collected at Elk Creek Falls Recreation Area, Clearwater County, Idaho, displayed broad yellow bands, concolorous with the paranotal markings, along the caudal margins of tergites 12–17. The paranotal spots vary in color being white to cream-colored on specimens that I encountered in Multnomah County, Oregon, reddish-orange on ones from Stevens County, Washington, and bright lemon yellow on ones from Latah and Clearwater counties, Idaho.

On the gonopods, the size and degree of irregularity of the distal projection from the dorsal face of the prefemoral process varies considerably. In some males, the structure is much larger and more flattened than shown in figures 4–7, becoming a second, more distal, and unprotected shelf; in others, it is more irregular and convoluted, and occasionally the side margins curl upwards, forming lips and demarcating a narrow, elongate trough or groove. In still others, the tip of the projection bends or curves laterad. The apical gonopodal margin is as shown in figures 4–7 in all specimens except those from Stevens County, Washington, in which the entire margin, not just the lateral side, is bent dorsad. As there is only one sample with this configuration, I include it under *C. armata*, but future workers with access to more material may conclude that this condition is significant enough to warrant specific recognition.

In females, the size of the medial projection of the valves varies, some being very large and overshadowing the rest of the valves. The

receptacle in some females is larger than that of the syntype, extending ventrad along the lateral surface of the valves and partly enclosing the operculum as well as being cupped around the anterior and caudal surfaces. These receptacles are saddle or bowl-shaped, with the valves situated on top in a ventral depression.

Ecology—The specimens that I collected in Multnomah County, Oregon, were wandering over the substrate in deciduous forests; those from Stevens County, Washington, were under partly buried, "stuck," pine and fir logs and detached pieces of bark beside a dirt driveway in a predominantly pine woods; and those from Latah and Clearwater counties, Idaho, on and under logs, moss, and leaves. Specimens from Chelan County, Washington, were also found "active on ground." Labels with preserved samples indicate that *C. armata* has been encountered in willow litter, under rocks and fungi, under logs near streams, under rotten logs, on moist hillsides, and under cow dung.

Distribution—Occurring in five segregated areas in the northwestern United States: the lower Willamette Valley of Oregon, the eastern slope of the Cascade Mountains in central Washington, the western slope of the Blue Mountains, northern Idaho and western Montana, and an isolated site in Stevens County, Washington (Figs. 68, 70). Specimens were examined as follows:

OREGON: *Benton Co.*, ca. 16 mi (25.6 km) N Corvallis, Finley Natl. Wildlife Ref., 7M, F, 31 March 1972, L. Russell (VMNH) and 2M, F, 26-28 April 1978, D. R. Breakey (WU). *Polk Co.*, Zena, 4-H Camp, M, 23 April 1983, D. R. Breakey (WU). *Marion Co.*, 2.5 mi (4.0 km) W Mehama, 4M, 2F, 30 March 1969, R. L. Westcott (UCD). *Clackamas Co.*, West Linn, MM, FF, 6 May 1972, L. Russell (VMNH). *Multnomah Co.*, Portland, 2M, 19 June 1882, L. Henshaw (MCZ); South Portland, M, May 1905, J. E. Benedict (NMNH); and Columbia River Gorge, Oneonta Trail between Horsetail Falls and Oneonta Gorge, M, 2 June 1991, R. M. Shelley (NCSM) and John B. Yeon St. Pk., along trail to Elowah Falls, 4M, 3 June 1991, R. M. Shelley (NCSM). *Umatilla Co.*, jct. N and S Forks, Umatilla R., M, 6 July 1967, F. A. Coyle (WAS); 3.0 mi (4.8 km) NE Gibbon, along Umatilla R., M, 7 July 1967, F. A. Coyle (WAS); 10.0 mi (16.0 km) E Ukiah, Bear Wallow Cpgd. along OR hwy. 244, M, 7 July 1967, F. A. Coyle (WAS). *Grant Co.*, vic. of Canyon City, M, 2F, October 1871, O. Harger, G. H. Collier (PMNH) TYPE LOCALITY.

WASHINGTON: *Stevens Co.*, along Springdale to Hunters Rd., 13.5 mi (21.6 km) W jct. WA hwy 231, 6M, 4F, 1 June 1993, R. M. Shelley (NCSM). *Chelan Co.*, Soda Spring, ca. 7.9 mi (12.6 km) W

Telma, 47.858°N, 120.968°W, M, 20-22 June 1974, R. Crawford (UWBM); Wenatchee Ridge, ca 7.2 mi (11.5 km) W Telma, 47.860°N, 120.959°W, M, F, 20 June 1974, R. Crawford (UWBM); along Roaring Creek, ca 6.5 mi (10.4 km) W Entiat, 47.687°N, 120.335°W, M, 15 June 1985, R. Crawford (UWBM); along Entiat Summit Road, ca 7.9 mi (12.6 km) N Cashmere, 47.638°N, 120.440°W, 2M, 2F, 12 June 1982, R. Crawford (UWBM); along US hwy. 2 ca 11.9 mi (19 km) N Leavenworth, 4M, 24 April 1988, C. S. Guppy (RBCM); and along US hwy. 2, ca 10 mi (16 km) N Leavenworth, Tumwater Cpgd., 6M, 4F, 18 August 1990 R. M. Shelley (NCSM). *Kittitas Co.*, Cle Elum, 47.15°N–25°N, 120.90°W, M, 9 May 1953, J. J. Gevers (UWBM); Thorp, 47.0°N, 120.6°W, M, 22 May 1954, Kilpatrick (UWBM); 5 mi (8 km) W Ellensburg, F, 4 June 1940, E. F. Dailey (UWBM); beside Yakima R. opposite Ellensburg, 3M, 8 July 1882, S. Henshaw (MCZ); and mouth of Moonlight Cyn., ca. 7 mi (11.2 km) W, 3.4 mi (5.4 km) N Thorp, 47.119°N, 120.822°W, M, 25 May 1986, R. Crawford (UWBM). *Yakima Co.*, Taylors, Wenas Valley, M, 6 July 1882, S. Henshaw (MCZ); and White Swan, M, 7 May 1938, W. W. Baker (NMNH).

IDAHO: *Kootenai Co.*, locality unspecified, M, September 1890, Leiberg (NMNH); 4th of July Cyn., M, 12 August 1929, R. V. Chamberlin (NMNH); and Medimont, 3M, F, 23 June 1957, H. S. Dybas (FMNH). *Benewah Co.*, 4 mi (6.4 km) SE Emida, M, 3F, 16 April 1987, R. S. Zack (WSU). *Shoshone Co.*, mouth of Eighty Day Cr., 1.3 mi (2.1 km) up Steamboat Cr. from mouth at Coeur d'Alene R., M, 23 May 1975, F. W. Grimm (CMN); and 8 mi (12.8 km) ENE Clarkia, Hobo Cedar Grove, 4M, 12 June 1985, W. Suter (UWY). *Latah Co.*, Laird Park, 8 mi (12.8 km) NE Harvard, Idaho Panhandle Nat. For., M, 9 June 1982, R. S. Zack (WSU) and 3M, F, 4 June 1993, R. M. Shelley (NCSM); 4.5 mi (7.2 km) N, 8.5 mi (13.6 km) E Harvard, Cleveland Gulch, M, F, 16 September 1978, A. K. Johnson (NCSM); 3 mi (4.8 km) N, 6.5 mi (10.4 km) E Harvard, along Blue Jacket Cr., M, 15 September 1978, A. K. Johnson (NCSM); nr. Harvard, Idaho Panhandle Nat. For., 2M, 22 July 1934, B. Malkin (CAS, WSU); E of Bovill, along Bob's Cr., F, 30 May 1985, C. Rogers (WSU); and 6 mi (9.6 km) E Bevrit, along Roger's Cr., 4M, F, 20 May 1986, along Roger's Cr., 4M, F, 20 May 1986, R. S. Zack (WSU). *Clearwater Co.*, Elk Cr. Falls Rec. Area E of Bovill, 2F, 8 August 1991, and 4M, 2F, 4 June 1993, R. M. Shelley (NCSM); 3.5 mi (5.6 km) N, 6.4 km (4.0 mi) E Headquarters, along Middleton Cr., 13M, 13 August 1978, A. K. Johnson (NCSM); 3.5 mi (5.6 km) N, 7.0 mi (11.2 km) W Pierce, 8M, 2F, 25 June 1978, A. K. Johnson (NCSM); and Greer, 2F, 30 August 1959, W. J. Gertsch, V. Roth (NMNH). *Idaho Co.*, 6.0 mi

(9.6 km) E, 9.0 mi (14.4 km) S Pierce, 0.5 mi (0.8 km) N Austin Ridge Lookout, 4M,2F, 30 June 1978, and 15M, 2F, 29 July 1978, A. K. Johnson (NCSM); 10.5 mi (16.8 km) E, 6.0 mi (9.6 km) S Pierce, Knoll Cr. Cyn., 2M, 3F, 25 August 1978, A. K. Johnson (NCSM); 13.0 mi (20.8 km) SSE Pierce, Eldorado Ridge, 2M, 18 July 1978, and 2M, 3F, 25 August 1978, A. K. Johnson (NCSM); 3.0 mi (4.8 km) W Lowell, M, 18 July 1963, W. F. Barr (FSCA); and Lowell, M, F, 4 July 1949, C. O. Bowles (NMNH).

MONTANA: *Sanders Co.*, 1.0 mi (1.6 km) W Noxon, 2M, F, date unknown, R. Schmitt (NMNH, FSCA); Thompson Falls, 5M, F, 16 August 1967, J. R. Helfer (UCD); and 3.0 mi (4.8 km) SSE Thompson Falls, Clark's Peak, Lolo Nat. For., 5M, 4 July 1950, B. Malkin (CAS, NMNH, WSU). *Missoula Co.*, Missoula, M, 7 July 1950, B. Malkin (NMNH).

The following literature record is considered accurate and indicated by the open symbol in figure 68.

WASHINGTON: *Whitman Co.*, Madson (misspelled as Madison), ca. 3 mi (4.8 km) W, 1 mi (1.6 km) S of Viola, Latah Co., ID (Chamberlin 1911).

Remarks—Hoffman (1979) suggested that the then five nominal species of *Chonaphe*—*armata*, *cygneia*, *patriotica*, *remissa*, and *serratus*—might be subspecifically related, and I (Shelley 1990) suggested that the genus might be monotypic with all these names synonyms of *armata*. However, the unpublished record that I cited from King County, Washington, is referrable to *C. remissa*, and the one from Stevens County, Washington, is a misidentification of a new species, *C. schizoterminalis*.

The newly cited records from Umatilla County, Oregon, are in the Blue Mountains of eastern Oregon and corroborate my conclusion (Shelley 1993*b*) that the type locality is in this range. In May 1993 I spent two days in the vicinity of Canyon City, Grant County, the presumptive type locality, attempting without success to confirm the occurrence of *C. armata* in the southern Blue Mountains. This area has been drastically altered by lumbering, and the only remaining hardwoods are narrow willow and alder thickets along creeks. The predominant vegetation is pine, and most of the southern Blue Mountains are unsuitable for xystodesmids, which occur primarily in hardwood associations. When Harger collected the types in October 1871, there was surely an extensive hardwood community in the broad John Day River Valley near the present towns of Mt. Vernon, John Day, and

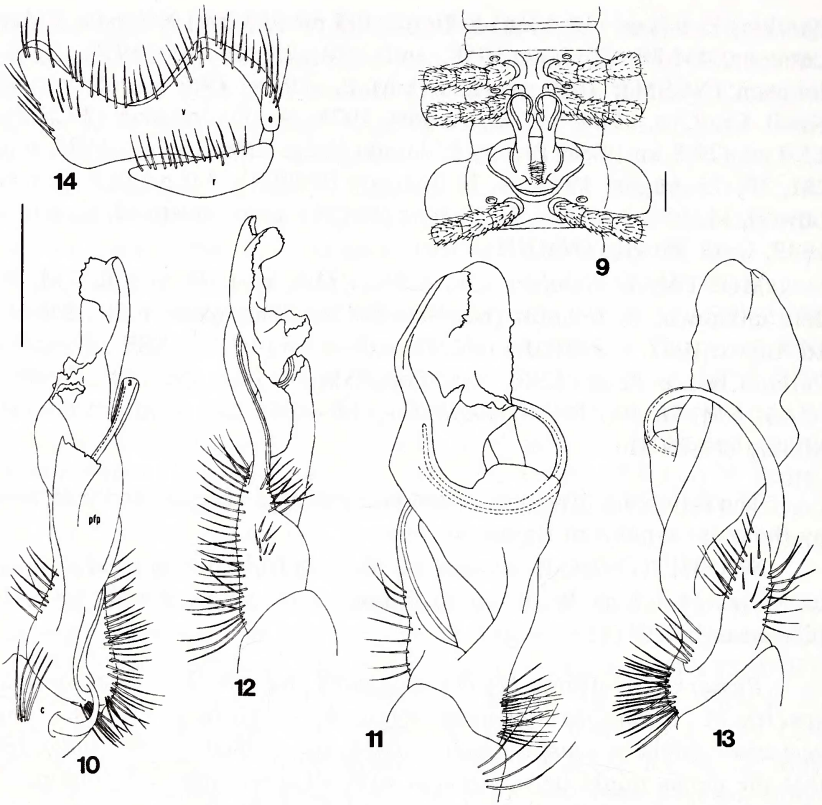


Fig. 9-14. *Chonaphe remissa*. 9, gonopods *in situ*, ventral view of male from King County, Washington. 10, left gonopod of holotype, medial view. 11, telopodite of the same dorsal view. 12, the same, lateral view. 13, the same, ventral view. 14, left cyphopod of female from Skamania County, Washington, caudal view. Abbreviations as in Figs. 2-8. Scale line for Fig. 9 = 1.00 mm; line for other Figs. = 1.30 mm for 10-13, 1.00 mm for 14.

Prairie City, and also along Canyon Creek, a fast-running tributary that flows through Canyon City and enters the main river at John Day. Staying in Canyon City (Shelley 1993*b*), Harger probably did not have to go far to find his new millipeds and centipede, but in May, I drove all the major highways and many back roads in the vicinities of these towns without finding any of the species or even suitable habitat. Consequently, the record of *C. armata* from Grant County in the southern Blue Mountains (Fig. 68) may reflect more of the historical range than present occurrence.

Chonaphe remissa Chamberlin

Figs. 9–14

Chonaphe armata: Attems, 1931:65–67, figs. 100–101; 1938 (in part):156, fig. 177. Verhoeff, 1941:fig. 5.

Chonaphe remissa Chamberlin, 1949:127, figs. 4–5. Chamberlin and Hoffman, 1958:27. Kevan, 1983:2968.

Type specimen—Male holotype (NMNH) collected by W. W. Baker, 2 May 1933, at Puyallup, Pierce County, Washington.

Diagnosis—Dorsal surface of prefemoral process with broad, thickened, irregular projection distal to shelf; apical margin slanting laterad, lateral side with vertical lamina lying along axis, marginally serrate; shield connecting with inturned lateral margin.

Color in life—Unknown, but evidence of light paranotal spots on preserved specimens.

Holotype—Length 24.5 mm, maximum width 5.3 mm, W/L ratio 21.6%, D/W ratio 75.5%.

Somatic features agreeing with those of *C. armata*, with following exceptions:

Epicranial suture distinct, terminating just above interantennal region. Width across genal apices 3.2 mm, interantennal isthmus 1.1 mm. Antennae reaching back to midlength of 4th tergite, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae with distinct central impressions. Facial setae as follows: epicranial 2-2, suprantennal 1-1, interantennal 1-1, subantennal 1-1, frontal 1-1, genal 1-1, clypeal about 11-11, labral about 14-14, merging with clypeal series and continuing for short distance along genal margins, about 3 setae per side.

Sides of metazonites with low, variable ridges above coxae on pregonopodal segments. 4th sternum with moderately large, medially coalesced projections between 3rd legs, length subequal to widths of adjacent coxae; 5th sternum with two shorter, widely separated projections between 4th legs and slight depression between 5th legs. Prefemora of legs on segments 15–18 with distinct distoventral spines, longest on segments 16–17.

Gonopodal aperture extending caudad between 9th legs, 1.8-mm wide and 0.9-mm long at midpoint, without indentations, sides elevating strongly caudad and continuing onto caudal extension. Gonopods *in situ* (Fig. 9, not this specimen) extending anteriad from aperture over segment 6 and the caudal part of segment 5. Gonopod structure as follows (Figs. 10-13): Coxae with linear fields of 5–8 macrosetae; sterna with moderate-size lobes subtending coxae. Prefemoral process arising from anteromedial surface, narrow basally, expanding greatly

at 1/4 length into ledge or shelf on dorsal side, outer margin extending beyond surface of ledge as translucent shield, tapering toward and connecting with inturned lateral margin, stem of prefemoral process continuing distad with lightly serrate margins, with broad, thickened, irregularly convoluted projection from caudal surface, apical margin slanting laterad, with perpendicular, marginally serrate lamina projecting from dorsal surface lateral to midline. Acropodite arising on caudolateral side of prefemur, looping around prefemoral process and curling onto shelf, curling distad and terminating behind lateral extension of shield.

Female from Skamania County, Washington—Body fragmented, length unmeasurable, maximum width 5.9 mm, D/W ratio 71.4%. Agreeing closely with holotype in structural details, except paranota more strongly declined, creating appearance of more vaulted body. Valves (Fig. 14) moderately large, moderately hirsute, medial corners strongly elevated, subtending deep central depression. Receptacle small, situated directly beneath or dorsal to valves on lateral side, hirsute along ventral surface, extending slightly around caudal side of latter but not around anterior side.

Variation—As in *C. armata*, the size and degree of irregularity of the distal projection of the prefemoral process varies, being larger and more convoluted in some males. The sides of the projection occasionally have variable teeth that project above the flattened distal surface, which may be level or slant downward. The shield curves distad and continues for varying distances beyond the shelf, connecting with the inturned lateral margin. In some males, this continuation extends to the distal extremity of the prefemoral process, where it is very narrow and indistinct; in others, the continuation ends near the level of the distal projection, and the inward curving lateral margin distal to this point is separate.

Ecology—The specimen from Mason County was taken from sabal/alder litter at the edge of a marsh; that from Grays Harbor County was found on a canyon wall; and those from Ape Cave, Skamania County, were recovered from a pitfall trap just inside the main entrance.

Distribution—Washington west of the crest of the Cascade Mountains. Specimens were examined as follows:

WASHINGTON: *King Co.*, Seattle, M, 9 April 1936, E. F. Dailey (UWBM); and Snoqualmie Falls, M, 19 May 1933, M. H. Hatch (FSCA). *Pierce Co.*, Puyallup, M, 2 May 1933, W. W. Baker (NMNH) TYPE LOCALITY. *Mason Co.*, Dennie Ahl Seed Orchard, ca. 5 mi (8 km) W Potlach, 47.379°N, 123.257–259°W, M, 6 May 1986, R. Crawford (UWBM). *Grays Harbor Co.*, along Canyon River, ca. 7.0 mi (11.2 km) WNW Matlock, nr. Mason Co. line, 47.262°N, 123.526°W, M, 29

August 1976, J. T. Thompson (UWBM). *Skamania Co.*, Ape Cave, ca. 4.4 mi (7.0 km) E, 4.0 mi (6.4 km) N Cougar (in Cowlitz Co.), 46.109°N, 122.210°W, M, F, 13–30 May 1983, R. Crawford (UWBM).

The following literature record of *C. armata* is referrable to *C. remissa*.

WASHINGTON: *Thurston Co.*, farm near Olympia (Attems 1931); Verhoeff's gonopod illustration (1941, fig. 5) is of this specimen.

Remarks—Most prior records of *C. armata* actually refer to *C. remissa*, as no one realized that the Cascade Mountains in Washington form a distributional boundary, with a different species on each side of the crest. An addition to the above record is the general comment by Loomis and Schmitt (1971) that *C. armata* occurs in the Puget Sound area. However, south of the Columbia River in Oregon, *C. armata* occurs in the Willamette Valley and eastern slope of the Coast Range, and both the genus and tribe are absent from the Cascades.

The prefemoral processes of *C. armata* and *remissa* are very similar and can be confused but the apical lamina is vertical or coaxial with the stem in the latter and horizontal or transverse to it in the former. Additionally, the thickened, convoluted, distal projection is more proximal in C. *remissa*, being closer to the shelf/shield and farther from the tip; in *C. armata*, it is situated closer to the tip, occurring almost in the middle between the shelf and tip. The shield is longer in *C. remissa*, extending well along the lateral side of the stem of the prefemoral process; it terminates at the level of the shelf in *C. armata*.

Chonaphe evexa, new species

Figs. 15–20

Type specimens—Male holotype and 1 male and 1 female paratypes (UCD), and 1 male paratype (NCSM), collected by J. S. Buckett and M. R. Gardner, 11 March 1968, 9 mi (14.4 km) north of Agness, Coos County, Oregon.

Diagnosis—Dorsal surface of prefemoral process without projection distal to shelf, with angular ridge; apical margin broadly rounded, continuing downward to blunt termination on medial side, not divided but with subterminal lateral margin inturned to narrowly rounded, subacuminate tip; shield not connecting with lateral margin.

Color in life—Unknown, but evidence of paranotal spots in preserved specimens.

Holotype—Length 21.5 mm, maximum width 3.4 mm, W/L ratio 15.8%, D/W ratio 82.4%.

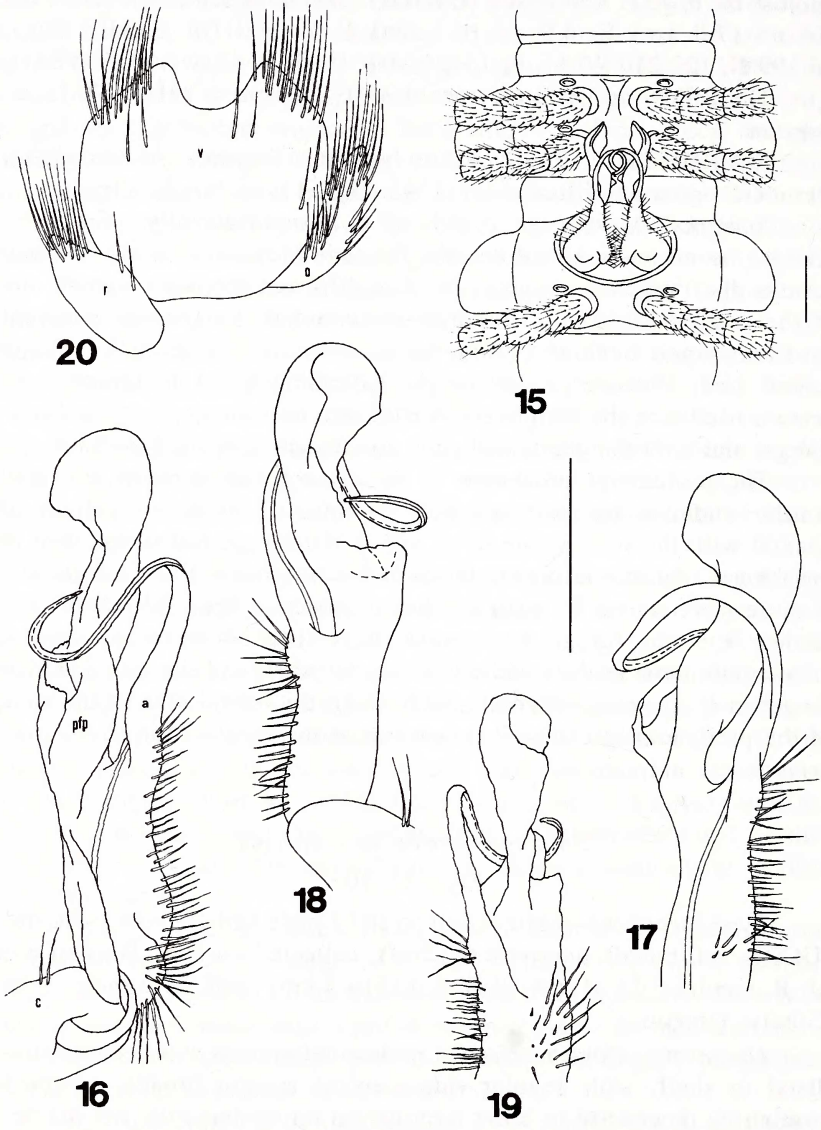


Fig. 15-20. *Chonaphe evexa*. 15, gonopods *in situ*, ventral view of paratype. 16, left gonopod of holotype, medial view. 17, telopodite of the same, dorsal view. 18, the same, lateral view. 19, the same, ventral view. 20, left cyphopod of female paratype, caudal view. Abbreviations as in Fig. 2-8. Scale line for Fig. 15 = 1.00 mm; line for other Fig. = 1.00 mm for 16-18, 1.20 mm for 19, 0.60 mm for 20.

Somatic features agreeing with those of *C. armata*, with following exceptions:

Epicranial suture faint, becoming more distinct and deeply impressed near termination above interantennal region. Width across genal apices 1.9 mm, interantennal isthmus 0.8 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae with faint impressions. Facial setae as follows: epicranial 2-2, interantennal 1-1, frontal 1-1, genal 3-3, clypeal about 7-7, labral about 11-11.

Collum moderately broad, ends terminating just above those of succeeding tergite. Paranota moderately developed, broadest on segments 1–5, angling ventrolaterad and continuing slope of dorsum, anterior corners blunt on segments 2–3, rounded on remaining tergites, caudolateral corners with suggestions of teeth on 2–3, rounded on remaining segments. Peritremata moderately distinct, moderately elevated above paranotal surface; ozopores located near midlength, opening laterad.

Sides of metazonites smooth, without ridges or impressions. 4th sternum with two minute, widely segregated knobs; 5th sternum with two flattened ridges between 4th legs and moderate depression between 5th legs. Prefemor of legs on segments 14–17 with short, ventrodistal spines.

Gonopodal aperture without caudal extension between 9th legs, 1.0-mm wide and 0.5-mm long at midpoint, without indentations, anterior margin flush with metazonal surface, sides elevating caudad and continuing onto caudal margin. Gonopods *in situ* (Fig. 15, of paratype) with telopodites extending anteriad from aperture in parallel arrangement, overhanging 6th sternum. Gonopod structure as follows (Figs. 16–19): Coxae relatively small, with two macrosetae, sternum with a short lobe subtending each coxa. Prefemoral process arising from anterior margin, narrow basally and curving slightly bisinuately, expanding at 1/4 length into shelf, outer margin extending beyond shelf as translucent shield, latter angling upward and merging imperceptibly with lateral margin of stem, stem without distal projection, with curvilinear ridge angling distolaterad from level of shelf to near lateral margin, outer/lateral margin curving to broadly rounded apex, subterminal edge slightly inturned to subacuminate tip, inner margin broadly indented, apical margin curving downward to narrowly rounded tip. Acropodite arising from caudal edge of prefemur, looping around prefemoral process and curling above shelf, displaced distad, normally curling onto shelf and terminating behind shield.

Male paratypes—The male paratypes agree with the holotype in all particulars.

possible. Agreeing closely with males in somatic features, except paranota more strongly declined, creating appearance of more highly arched body. Valves (Fig. 20) relatively small, corners extending slightly ventrad for equal distances, subtending deep central depression, with dense hair patches arising from medial and lateral projections. Receptacle relatively small, flat, and inconspicuous, with long hairs arising from ventral margin, extending slightly beyond anterior and caudal surfaces of valves, but not cupped around latter.

Distribution—Known only from the type locality.

Remarks—This intriguing species exhibits several distinct somatic features. As shown by the lower W/L ratio, *C. evexa* is longer and narrower than either *C. armata* or *remissa*, a distinction that is made even more dramatic in side by side comparisons because of its smaller, more rounded paranota. The gonopodal aperture does not extend caudad between the 9th legs, in marked contrast to the conditions in both *C. armata* and *remissa*, and the gonopods are oriented slightly differently *in situ*. In *C. evexa*, the acropodite arises almost centrally on the caudal side, as opposed to a sublateral origin in the other species. Consequently, the telopodite is rotated slightly counter-clockwise and is situated differently on the coxa. Occurring in the Coast Range of southwestern Oregon, *C. evexa* is well isolated from the main generic distribution, as the most proximate locality for *C. armata*, in Benton County, is some 144 mi (230 km) to the north-northeast.

Chonaphe schizoterminalis, new species

Figs. 21–26

Type specimens—Male holotype, one female paratype, and an additional segment of a male with gonopods (MCZ) collected by R. V. Chamberlin on an unknown date at Springdale, Stevens County, Washington.

Diagnosis—Dorsal surface of prefemoral process without thickened projection distal to shelf, with angular, laminate flap overlapping shield; apical margin gently curved and continuing downward to acuminate termination on medial side, strongly divided with lateral side extending inward to subacuminate tip as dactyliform projection; shield connecting with inturned lateral margin.

Color in life—Unknown, specimens completely blanched by preservative.

Holotype—Length 16.1 mm, maximum width 2.9 mm, W/L ratio 18.0%, D/W ratio 82.8%.

Somatic features agree with those of *C. armata*, with the following

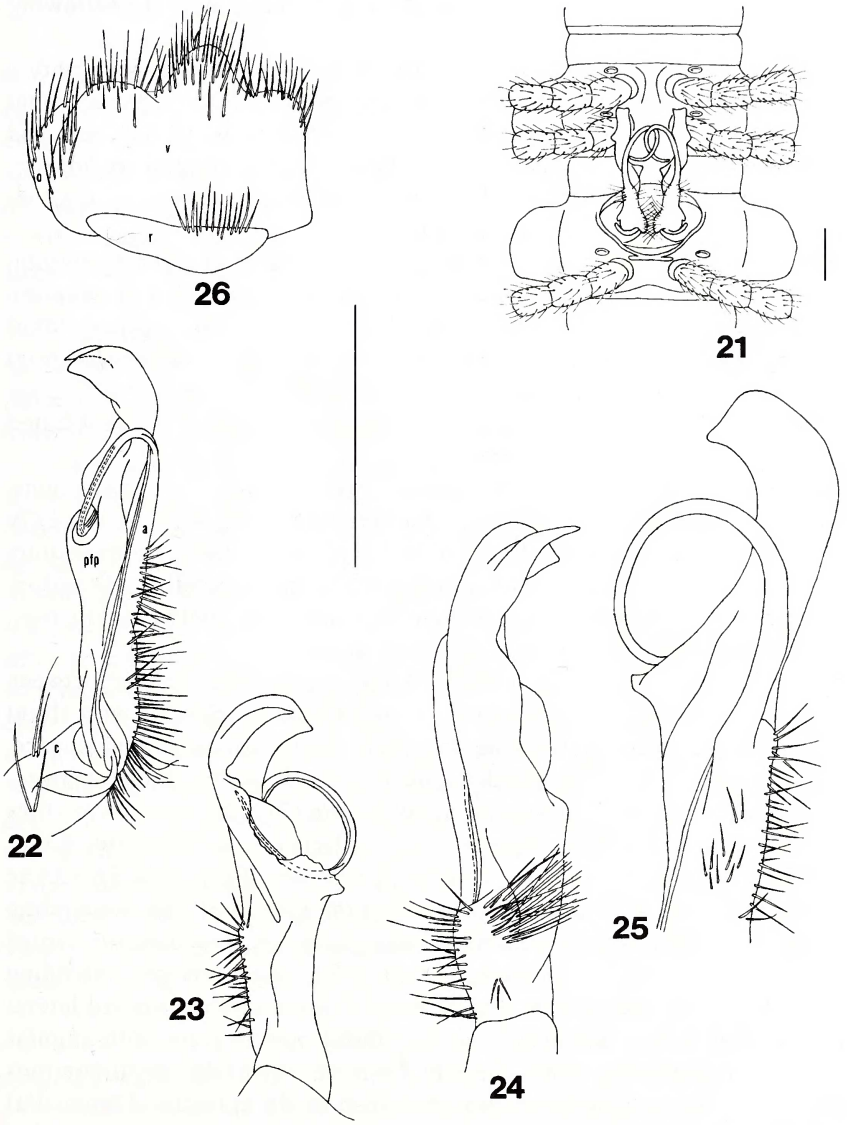


Fig. 21-26. *Chonaphe schizoterminalis*. 21, gonopods *in situ*, ventral view of paratype. 22, left gonopod of holotype, medial view. 23, telopodite of the same, dorsal view. 24, the same, lateral view. 25, the same, ventral view. 26, left cyphopod of female paratype, caudal view. Abbreviations as in Figures 2-8. Scale line for Figure 21 = 1.00 mm; line for other Figures = 1.25 mm for 22 and 24-25, 1.66 mm for 23, 1.00 mm for 26.

Somatic features agree with those of *C. armata*, with the following exceptions:

Epicranial suture thin but distinct, terminating just above interantennal region. Width across genal apices 2.2 mm, interantennal isthmus 0.5 mm. Antennae broken at articulations of 1st and 2nd articles. Genae with shallow central impressions. Facial setae as follows: epicranial 2–2, interantennal 1–1, subantennal 1–1, frontal 1–1, genal 3–3, dypeal about 12–12, labral about 16–16.

Collum broad, ends terminating above those of succeeding tergite. Paranota moderately developed, broadest on segments 1–5, angling ventrolaterad and continuing slope of dorsum, anterior corners blunt on segments 2–3, rounded at best on remaining tergites, caudolateral corners blunt on 2–3, rounded on remaining segments. Peritremata distinct, strongly elevated above paranotal surface; ozopores located near midlength, opening laterad.

Sides of metazonites with variable shallow grooves and impressions, without ridges. 4th sternum with two paramedial projections, medially coalesced, slightly longer than widths of adjacent coxae; 5th sternum with two shorter, widely segregated projections subtending 4th coxae, shorter than widths of latter, moderately depressed between 5th legs. Prefemora of all legs without traces of spines.

Gonopodal aperture extending slightly caudad over sternum between 9th legs, about 1.3-mm wide and 0.6-mm long at midpoint, with slight anteriolateral indentations, anterior margin flush with metazonal surface, sides elevating strongly caudad and continuing onto caudal margin, lowering slightly in midline. Gonopods *in situ* (Fig. 21) with telopodites extending anteriad from aperture in parallel arrangement, overhanging 6th sternum. Gonopod structure as follows (Figs. 22–25): Coxae relatively small, with 2 macrosetae; sternum with short lobe subtending each coxa. Prefemoral process arising from anterior margin, broad basally, expanding at 1/4 length into shelf, outer margin extending beyond latter as translucent shield, latter angling upward toward lateral margin and fading out imperceptibly, distal part of stem with angular laminate flap folding over shield to form enclosed tube, stem continuing distad, apically divided and curving broadly apically, distomedial margin strongly indented, distolateral margin expanding distad, leaning over stem, and continuing as acuminate dactyliform projection, subequal in length to that of medial margin. Acropodite arising from caudal margin of prefemur, looping above medial surface of prefemoral process and curling onto shelf, extending through enclosure formed by flap and shield, emerging distad and terminating behind inturned lateral margin.

Paratype gonopods—Agreeing with those of holotype in all details.

Female paratype—Length about 24.7 mm, maximum width 3.4 mm, W/L ratio 13.8%, D/W ratio 82.4%. Agreeing closely with male in somatic features, except paranota shorter and more strongly declined, creating appearance of more vaulted body. Valves (Fig. 26) moderate-size, hirsute along ventral margins with moderate-size lobes at midlength of ventral surfaces, without depressions. Receptacle small flat, and inconspicuous, located directly beneath valves, not cupped around sides of latter, with a few hairs from ventral margin.

Distribution—Known only from the type locality.

Remarks—Neither of the complete specimens is in good condition, having softened after years in preservative. There is also an additional, loose reproductive segment of a male with both gonopods intact. I have labeled these as "male paratype gonopods."

The smallest species, *C. schizoterminalis* is somewhat broader in proportion to its length than *C. evexa*. It is unique in the complete absence of prefemoral spines on the walking legs, and like *C. evexa*, the gonopodal telopodites are rotated counterclockwise on the coxa, in contrast to the condition in *C. armata* and *remissa*. However, *C. schizoterminalis* shares the caudal expansion on the aperture with the last two species. Northeastern Washington has been very poorly sampled, as most collectors have focused on the wet coastal forests west of the crest of the Cascades. Additional unexpected millipeds may therefore await discovery in the Okanogan, Colville, and Kaniksu National Forests in Okanogan, Ferry, Stevens, and Pend Oreille counties, and *C. schizoterminalis* could conceivably occur across the International Border near Rossland and Trail, British Columbia, only 71.5 mi (113.8 km) to the north. I visited the Springdale area in May 1993 to try to obtain more material, but encountered *C. armata*, not *C. schizoterminalis*, approximately 13.5 mi (21.6 km) west of the village along the Springdale to Hunters road.

Genus *Semionellus* Chamberlin

Semionellus Chamberlin, 1920:97. Attems, 1938:200. Chamberlin and Hoffman, 1958:47. Jeekel, 1971:287. Hoffman, 1979:157. Kevan, 1983:2968.

Type species—Polydesmus (*Leptodesmus*) *placidus* Wood, 1864, by original designation.

Diagnosis—Paranota present on all segments but becoming progressively less distinct caudad, caudal part of body appearing subcylindrical; epiproct without constriction; gonocoxae widely segregated by narrow sternal band, latter with lateral lobes; telopodal elements

subparallel for most of lengths, arising distad on prefemur; prefemoral process long, expanded and laminate, elaborately ornamented, with strong medial spine distal to midlength and numerous hairs on lateral surface and inner distal and apical margins; acropodite acicular, passing through essentially a single vertical plane, sublinear for most of length, lying over medial face of prefemoral process; cyphopod valves flattened ventrad, without lobes, projections, or cavities.

Description—A genus of moderate-size to large chonaphine Xystodesminae with the following characteristics:

Body composed of head and 20 segments in both sexes. Head of normal appearance, smooth. Epicranial suture sharp, distinct. Antennae relatively short and broad, with 4 conical, terminal sensory cones; no other sensory structures apparent. Facial setae with epicranial, subantennal, frontal, clypeal, and labral series; interantennal and genal absent.

Terga smooth, polished; strictures broad, distinct. Collum large and broad, terminating at same level as succeeding tergite. Paranota present on all tergites, becoming distinctly shorter around midbody and progressively more so caudad, moderately declined, continuing slope of dorsum. Peritremata distinct; ozopores opening sublaterad.

Caudal segments normal for family.

Sides of metazonites smooth, polished, with at most only shallow impressions. Pregonopodal sterna of males glabrous; 4th with two long, diverging projections, overhanging adjacent coxae; 5th with two short lobes between 4th legs, flattened between 5th; 6th sternum strongly depressed between both leg pairs. Postonopodal sterna glabrous, flat, and unmodified, with only shallow transverse grooves originating between leg pairs. Coxae unmodified; prefemora with broadly rounded, ventrodistal lobes, becoming progressively smaller caudad.

Gonopodal aperture large, subtrapezoidal, with broad caudal extension between 9th legs. Gonopods *in situ* with telopodites in parallel arrangement. Coxae with 2–5 macrosetae, connected to each other by narrow sternal band, latter with lobes subtending coxae. Telopodal elements subparallel for most of lengths, arising distad on prefemur; latter relatively broad; prefemoral process large, expanded and laminate, elaborately ornamented, with broad, cupulate, irregularly serrate basal flange, bending abruptly dorsad and expanding into lateral and another medial flanges, former marginally smooth, narrowing or expanding distad, with or without thickened margin, latter cupulate basally, curling around acropodite in some males, marginally irregular and with strong distal spine, stem of process narrowing then expanding greatly distal to flanges to subacuminate tip on inner, distal corner, inner margin and lateral surface hirsute, becoming progressively denser distad, distal

margin indented. Acropodite long, slender, and aciciular, demarcated from prefemur by strong constriction, bending anteriad basally, sublinear for most of length, curving broadly distad, about 3/4 as long as prefemoral process. Prostatic groove arising in pit in prefemur, running down medial side of latter and curving onto lateral side of acropodite, curving around latter and continuing to terminal opening.

Cyphopod aperture long and narrow, encircling 2nd legs, sides and caudal margin elevated above metazonal surface, more so medially. Cyphopods *in situ* with valves oriented transversely in aperture, common surface visible in opening. Valves moderate-size, moderately hirsute, without marginal extensions and central depression. Receptacle moderate-size, ventrally hirsute, located on dorsomedial side of valves, not alate and cupped around latter. Operculum large, located on dorsolateral side of valves, with long apical hairs.

Distribution—Occurring in four segregated areas east of the Central Plains including parts of Minnesota and Wisconsin; the lower peninsula of Michigan, northwestern Ohio, and Indiana; one site in eastern Ohio; and parts of Maryland, West Virginia, and Virginia.

Species—One.

Remarks—The only tribal component east of the Plains, *Semionellus* is evidence of prior faunal linkage through the gap of some 1,053 mi (1,684 km) in the northcentral United States. The Black Hills in western South Dakota, an island of forested mountains in the midst of intervening grasslands, is a plausible site for an undiscovered, relict, chonaphine population that might bridge anatomical gaps between *Semionellus* and *Chonaphe*. However, my field trip there in May 1986 produced only parajulids and introduced species, and disclosed no xystodesmids, possibly because of unseasonably cold weather (Shelley 1990). Hardwood-fir environments in this area, particularly in Spearfish Canyon, the north slope of Mount Harney, and the Iron Creek drainage above the Needles Section of Custer State Park, should be reinvestigated in warmer weather to ensure that the Black Hills do not harbor xystodesmids. Inselberg ranges in Montana east of the Continental Divide like the Big and Little Belt Mountains and the Absaroka and Bighorn Ranges are other plausible areas for undiscovered chonaphines that would be remnants of the ancient faunal connection.

Semionellus placidus (Wood)

Figs. 27–32

Polydesmus (*Leptodesmus*) *placidus* Wood, 1864:9; 1865:225, fig. 56.
Polydesmus (*Leptodesmus*) *floridus*, var.? Wood, 1864:9; 1865:226.

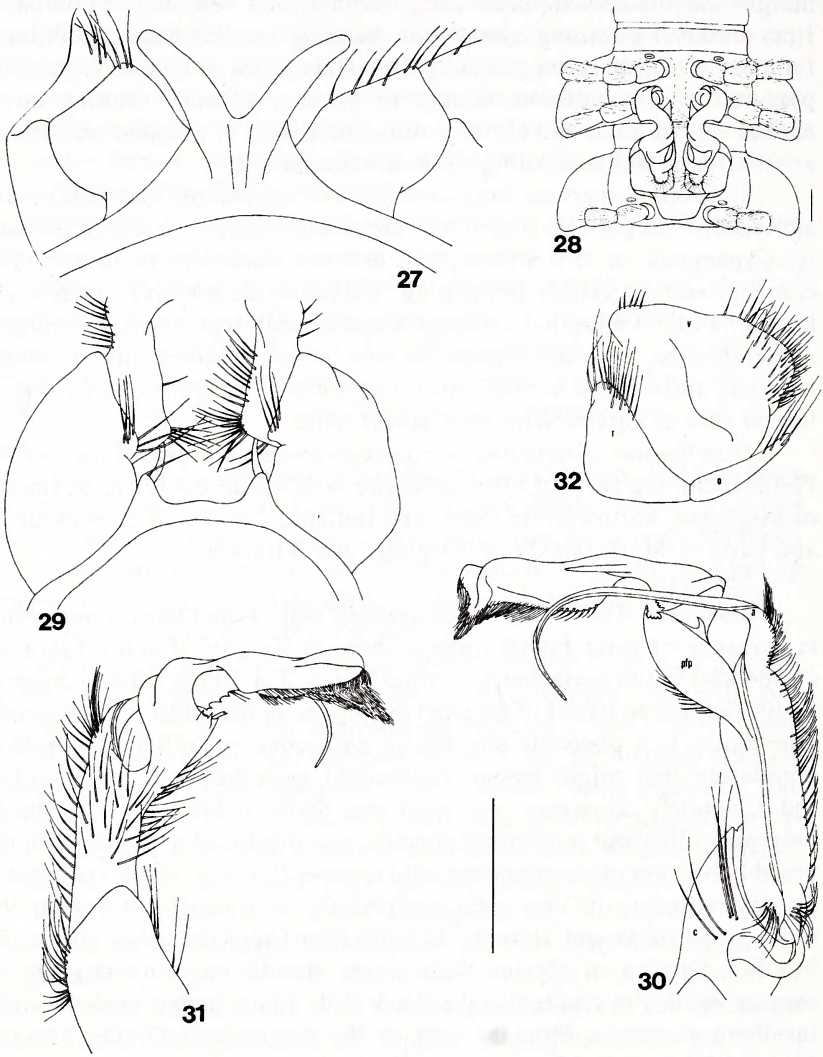


Fig. 27-32. *Semionellus placidus*. 27, 3rd sternum of male from Midland County, Michigan, caudal view. 28, gonopods *in situ*, ventral view of male from Tucker County, West Virginia. 29, gonocoxae and sternum of male from Midland County, Michigan, caudal view. 30, left gonopod of the same, medial view. 31, the same, lateral view. 32, left cyphopod of female from Pepin County, Wisconsin, caudal view. Abbreviations as in Fig. 2-8. Scale line for Fig. 28 = 1.00 mm; line for other Fig. = 1.40 mm for 27, 3.50 mm for 29-31, 1.00 mm for 32.

Leptodesmus placidus: Bollman, 1888:406; 1893:122. Carl 1903:549–551, Taf. 17, fig. 18. Williams and Hefner, 1928:110, fig. 11b.
Leptodesmus borealis Bollman, 1893:183–184.
Trichomorpha placida: Attems, 1938:119–120, fig. 139. Causey, 1952:9.
Chonaphe michigana Chamberlin, 1946:31–32, figs. 1-2.
Semionellus placidus: Chamberlin, 1947:24, fig. 3. Johnson, 1954:248, pl. III, fig. 19. Chamberlin and Hoffman, 1958:47–48. Kevan, 1983:2968.
Semionellus michiganus: Chamberlin, 1948:258.

Type specimen—Lost. The type locality is Michigan without further specification (Wood 1864, 1865).

Diagnosis—With the characters of the genus.

Color in life—Paranota red, metaterga black with concolorous red bands along the caudal margins.

Male from Midland County, Michigan (Holotype of C. michigana)—Length 28.3 mm, maximum width 4.8 mm, W/L ratio 16.7%, D/W ratio 77.1%.

Head capsule smooth, polished; epicranial suture distinct, terminating in interantennal region. Antennae appearing relatively short and broad, reaching back to caudal margin of 3rd tergite; relative lengths of antennomeres 2>3>6>4=5>1>7. Genae not margined laterally, with distinct central impressions, ends broadly rounded and extending slightly beyond adjacent cranial margins. Facial setae as follows: epicranial 2-2, interantennal, frontal, and genal not detected, clypeal about 10-10, labral about 14-14.

Collum moderately broad, ends not extending below those of succeeding tergite. Paranota well developed on anteriormost segments, becoming noticeably shorter on segment 9 and progressively shorter caudad, moderately declined, angling ventrolaterad and continuing slope of dorsum, anterior corners rounded, caudolateral corners blunt through segment 9, rounded thereafter. Peritremata broad, distinct, strongly elevated above apranotal surface; ozopores located caudal to midlength, opening sublaterad.

Sides of metazonites generally smooth, polished, with variably curved, shallow impressions. Strictures distinct. Gonapophyses moderately long and stout, extending moderately from 2nd coxa. Pregonopodal sterna glabrous, variably modified; 4th sternum with two long, diverging projections extending ventrolaterad and overlying 3rd coxa (Fig. 27); 5th sternum with two short, subconical, paramedian knobs between 4th legs, flat between 5th legs; 6th sternum strongly depressed to accommodate telopodites. Postgonopodal sterna glabrous, with bicruciform impressions, caudal margins gently curved, without modifications.

Coxae without projections; prefemora with broadly rounded lobes on outer surface, becoming smaller and less pronounced caudad; tarsal claws sublinear. Hypoproct broadly rounded, paraprocts with margins strongly thickened.

Gonopodal aperture very broad, subtrapezoidal, extending caudad between 9th legs and overhanging caudal margin of segment, with strong shelf in caudal extension, extending anteriad nearly to anterior margin of prozonum, latter with only thin sclerotized strip along anterior margin to maintain structural integrity, 2.4-mm wide and 2.1-mm long at midpoint, without indentations, sides elevated slightly above metazonal surface, inner margin continuing smoothly around bases of coxae, outer margin continuing into strong elevations along caudolateral and caudal margins, latter strongly thickened and slightly flared. Gonopods *in situ* (Fig. 28, not this specimen) with telopodites extending anteriad from aperture in parallel arrangement, overhanging 6th sternum. Gonopod structure as follows (Figs. 29–31): Coxa relatively large, with 2–5 macrosetae above cannula, connected to opposite member by narrow sternal band, latter with two moderate lobes subtending coxae. Prefemur relatively long and broad, expanding slightly distad, with large, laminate prefemoral process arising distad from anterior surface, expanded basally into broad, cupulate flange with strong spur on medial margin, several minute teeth in indentation on distal margin, and short, irregularly serrate projection laterally, stem of prefemoral process curving slightly then bending abruptly dorsad and expanding into second medial and a lateral flanges, medial flange widest basally and curving dorsad with minute marginal teeth and strong distal spine, lateral flange broadly rounded basally, extending distad into broad ledge overhanging tip, ledge with numerous short hairs, overhanging denser hairs on stem of prefemoral process, latter narrowing greatly distal to bases of flanges then expanding greatly on inner surface, inner margin hirsute and becoming progressively more so distad, expanding apically into subacuminate tip at inner distal corner, directed dorsad, apical margin broadly indented. Acropodite arising on caudomedial side of premur, demarcated by strong constriction, bending abruptly anteriad and continuing sublinearly parallel to stem of prefemoral process, curving broadly dorsad distally and narrowing to acuminate tip, overall length about 3/4 that of prefemoral process.

Female from Pepin County, Wisconsin—Length 27.4 mm, maximum width 4.4 mm, W/L ratio 16.1%, D/W ratio 84.1%. Agreeing closely with males in somatic details except paranota more strongly declined, creating appearance of more highly arched body. Cyphopods *in situ* with valves oriented transversely in aperture, common surface

visible in opening. Valves (Fig. 32) relatively large, subequal, ventral surfaces flat, without depression, margins not extended, moderately hirsute. Receptacle moderately large, located at dorsomedial corner of valves, not alate, not cupped around latter, with long hairs arising from ventral surface.

Variation—The only noteworthy gonopodal variation concerns the degree of serration on the medial flanges, which can be more or less than on the illustrated specimen and quite jagged on occasional males, and the thickness of the distolateral ledge, whose margin is thickened on some males and expanded slightly into a rim lying perpendicular to the axis of the prefemoral process. On a few males the acropodite lies closer to the stem of the prefemoral process, running through the curvature of the second medial flange. Facial setae on a male from Tucker Co., WV, are epicranial 2-2, interantennal absent, subantennae 1-1, frontal 1-1, clypeal about 12-12, labral about 18-18, merging with clypeal series and continuing for short distance along genal border, about 4 setae per side.

Ecology—I have collected *S. placidus* in West Virginia in deciduous forests and cove habitats under moist leaves near water sources.

Distribution—The only tribal representative occurring in the east, *S. placidus* inhabits four segregated areas. The western population traverses the Mississippi River in the Central Lowland Physiographic Province from southeastern Minnesota to southeastern Wisconsin and may not be contiguous, as linkage has not been demonstrated between the samples taken along the Mississippi and those in southern and eastern Wisconsin. The central population, also in the Central Lowlands, extends from the central part of the lower peninsula of Michigan, near the base of the "thumb," through western Ohio to western and south central Indiana. The eastern population, located in the Appalachian Plateau, Ridge and Valley, and Blue Ridge Physiographic Provinces, ranges from western Maryland through eastern West Virginia, to western Virginia, reaching its eastern periphery in Shenandoah National Park. There is also a single record from southeastern Ohio along the Ohio River. Approximate areas of the populations are 273 mi (437 km) east/west and 45 mi (72 km) north/south for the western, 245 mi (392 km) east/west and 332 mi (531 km) north/south for the central, and 98 mi (157 km) east/west and 137 mi (219 km) north/south for the eastern. The western and central populations are separated by around 156 mi (250 km), and the central and eastern populations are segregated by about 234 mi (374 km); the southeastern Ohio record is intermediate between the last two areas. No specimens have been encountered in

about 117 mi (187 km) from the closest site in Ontario, and *S. placidus* may eventually be discovered in Essex County, as was the rhysodesmine species *Pleuroloma flavipes* Rafinesque (Shelley 1988). However, in two days of searching in July 1986, including extensive investigations in Point Pelee National Park, I did not encounter it. Specimens were examined as follows:

MINNESOTA: *Rice Co.*, Northfield, Carleton College, M, F, Fall 1955, P. Jensen (VMNH). *Wabasha Co.*, Goodhue, Lake Pepin, 2M, 2F, 25 March 1931, W. J. Gertsch (VMNH). *Winona Co.*, 2 mi (3.2 km) NE Elba, F, 14 October 1973, B. Cutler (UMN); Whitewater St. Pk., M, 12 June 1961, H. W. Levi (MCZ); and Winona, juv., date unknown, Holzinger (NMNH). *Houston Co.*, Houston, M, 25 May 1940, C. E. Mickel (UMN).

WISCONSIN: *Pepin Co.*, Lake Pepin, 2M, 2F, 25 July 1931, W. J. Gertsch (NMNH). *Dane Co.*, Madison, M, 22 February 1914, A. S. Pearse (NMNH); and Bascom Woods nr. Madison, F, 30 September 1947, H. W. Levi (MCZ). *Ozaukee Co.*, Mud Lake, 2M, F, 9 April 1979, Hildebrandt, Plonczynski (MPM). *County Unknown*, "Bob's Cabin," 2M, 2F, 21 October 1973, P. Riemer (TMM).

MICHIGAN: *Midland Co.*, Midland, 2M, 25 May 1942 and 7 May 1943, R. R. Dreisbach (NMNH). *Ingham Co.*, East Lansing, Sanford Woodlot, M, F, 3 October 1955, collector unknown (FSCA). *Washtenaw Co.*, 5 mi (8.0 km) W Ann Arbor, M, 6 July 1948, G. C. Wheeler (FSCA). *Monroe Co.*, Monroe, 6M, 4F, July 1965, collector unknown (UCD).

INDIANA: *Benton Co.*, Boswell, M, F, date unknown, Mattier (NMNH). *Greene Co.*, Richland Cr., exact location unknown, 2F, 25 March 1952, collector unknown (FSCA). *Monroe Co.*, locality not specified, M, 12 August 1953, B. G. Owen (FSCA); Green's Bluff, exact location unknown, F, 1 November 1953, B. G. Owen (FSCA); along Wylie L., M, 12 July 1953, B. G. Owen (FSCA); and Morgan-Monroe St. For., 2F, 15 April 1952, collector unknown (FSCA). *Union Co.*, Whitewater St. Pk., 2F, 7 August 1953, B. G. Owen (FSCA).

OHIO: *Monroe Co.,* 1.8 mi (2.9 km) N Rinard Mills, nr. Knowlton Covered Bridge, F, 8 July 1986, D. R. Whitehead (NMNH).

MARYLAND: *Garrett Co.*, exact location unknown, M, July 1907, W. Stone, T. D. Keim, H. W. Fowler (ANSP).

WEST VIRGINIA: *Tucker Co.*, Lanesville, 5.5 mi (8.8 km) E WV hwy. 32, Monongahela Nat. For., 3M, F, 23 August 1978, R. M. Shelley, C. P. Withrow (NCSM); and Dolly Sods, 11M, 11F, 20 July 1986, D. R. Whitehead (NMNH). *Randolph Co.*, 2.1 mi (3.3 km) W Alpena, along US Hwy. 33, 14M, 5F, 23 August 1978, R. M. Shelley,

Alpena, along US Hwy. 33, 14M, 5F, 23 August 1978, R. M. Shelley, C. P. Withrow (NCSM); and S of Harman, along Dry Fork Rd., 7 mi (11.2 km) SW jct. Job Whitmer Rd., F, 23 June 1986, D. R. Whitehead (NMNH). *Pendleton Co.*, 4.5 mi (7.2 km) W Judy Gap, along Briery Gap Rd., M, 2F, 21 August 1988, D. R. Whitehead, L. A. Pereira (NMNH). *Pocahontas Co.*, Monongahela Nat. For., exact location unknown, M, 2F, 24 September 1972, W. A. Shear (WAS); and Hills Cr. Falls Scenic Area, along WV hwy. 55 E Greenbrier Co. line, F, 19 June 1972, W. A. Shear (WAS).

VIRGINIA: *Rockingham Co.*, 7 mi (11.2 km) NNW Rawley Springs, Tomahawk Mtn., F, 17 June 1988, K. A. Buhlmann (VMNH). *Warren Co.*, N end of Skyline Dr., Shenandoah Nat. Pk., M, 24 September 1943, collector unknown (NMNH). *Page Co.*, Luray, F, July 1966, C. Ewing (NCSM); Skyland, Shenandoah Nat. Pk., M, date unknown, J. P. E. Morrison (NMNH); and along Skyline Dr. at Stony Man Mtn., Shenandoah Nat. Pk., 7M, 3F, 29 May–11 June 1950, B. D. Burks (NMNH). *Page/Rappahannock Cos.*, along Skyline Dr., 1–2 mi (1.6–3.2 km) S Panorama, M, F, 21 June 1938, H. F. & E. M. Loomis (VMNH). *Madison Co.*, along Skyline Dr. above Hemlock Spgs. Overlook, Shenandoah Nat. Pk. 3M, 2F, 26 June 1953, L. Hubricht (VMNH); along Skyline Dr. at milepost 39, Shenandoah Nat. Pk., F, 13 July 1957, Highton, Barry (VMNH); and "Limberlost," Shenandoah Nat. Pk., 6M, 2F, 2 juvs., 27 May 1990, C. A. Pogue (VMNH). *Greene Co.*, along Skyline Dr. nr. milepost 71, Shenandoah Nat. Pk., F, 13 July 1957, Highton, Barry (VMNH). *Augusta Co.*, W side of Humpback Mtn., along Blue Ridge Pkwy. S of I-64, M, F, 17 June 1947, (VMNH). *Botetourt Co.*, nr. Sugarland, Apple Orchard Mtn., 2M, F, 27 May 1962, R. L. Hoffman (VMNH) and M, 14 October 1962, collector unknown (VMNH).

The following additional literature records are deemed valid and are denoted by open symbols in figure 69.

WISCONSIN: *Milwaukee Co.*, locality not specified (Causey 1952).

OHIO: *Allen*, *Hardin*, *Seneca*, and *Wood cos.*, localities not specified (Williams and Hefner 1928).

Deletions—The following literature records to either *S. placidus* or a synonym refer to other polydesmoids and hence are deleted.

KANSAS: *Jefferson Co.*, cited as *Polydesmus floridus* (Cragin 1885) and *Leptodesmus placidus* (Gunthorp 1913, 1921). No modern, authentic records are available from anywhere near Kansas, as shown in figures 1 and 69. These records of *P.* and *L. floridus* probably refer to a eurymerodesmid and were cited as such by Shelley (1989).

NEBRASKA: West Point, Roca, Rulo, and LaPlatte, cited as *L. floriaius* (Kenyon 1893*a*) and *L. floridus* (Kenyon 1893*b*). Shelley (1989) synonymized this usage of *L. floridus* with *E. mundus*.

GEORGIA: Ft. Benning (Chamberlin 1951). As noted by Shelley (1990), this record is a misidentification of *Oxidus gracilis* (Koch).

ILLINOIS: *Union Co.*, Rich's Cave near Cobden (Causey 1952). As this site is along the Mississippi River in southern Illinois, far from the range of *S. placidus*, this record of a juvenile surely refers to another xystodesmid.

Remarks—As noted by Shelley (1990), the northern- and western-most record of *S. placidus* is that from Rice County, Minnesota, and the southern- and eastern-most are in Botetourt and Madison counties, Virginia, respectively. These records span a distance of some 858 mi (1,381 km) in the east-west dimension and 429 mi (688 km) in the north-south. The Monroe County, eastern Ohio record, shown by a dot in figures 1 and 69, was obtained since my 1990 paper and lies nearly midway between the central and eastern faunal areas. This record may indicate the existence of a small additional population along the northern/western side of the Ohio River.

In addition to the narrower body, females of *S. placidus* can be distinguished from ones of other eastern taxa by the hirsute receptacle, as this cyphopodal structure is glabrous in the other eastern tribes.

Genus *Montaphe* Chamberlin

Montaphe Chamberlin, 1949:127. Chamberlin and Hoffman, 1958:38. Jeekel, 1971:273. Hoffman, 1979:157. Kevan, 1983:2968.

Type species—*Leptodesmus* (*Chonaphe*) *elrodi* Chamberlin, 1913, by original designation.

Diagnosis—Paranota present and distinct on all segments; epiproct without constriction; gonocoxae narrowly segregated by narrow sternal band, latter either with two paramedian lobes adjacent to coxae or single, broad, central lobe; telopodal elements parallel or subparallel for most of lengths, arising proximad on prefemur; prefemoral process variable, either long, extending well beyond acropodal loop, and narrowly blade-like, with strong distal barbules and a broad projection proximal to midlength, or short, terminating inside acropodal loop, and apically expanded and deeply divided; acropodite narrowly blade-like basally, acicular to subacicular distad, typically looping over prefemoral process, either without projections or expanding basally and with lateral spiniform projection; cyphopods with medial valves expanding gently to strongly ventrad, constituting at most only short lobes, subtending at most only moderate central cavity.

Description—A genus of moderately large chonaphine Xystodesminae with the following characteristics.

Body composed of head and 20 segments in both sexes, essentially parallel sided, tapering at both ends.

Head of normal appearance, smooth, polished. Epicranial suture faint or distinct, terminating above epicranial region. Antennae relatively short and broad, becoming progressively more hirsute distad, with 4 conical sensory cones on ultimate anticle, no other sensory structures apparent. Genae not margined laterally, with faint or distinct central impressions, ends broadly rounded and extending slightly beyond adjacent cranial margins. Facial setae with epicranial, genal, clypeal, and labral series, with or without frontal and subantennal series, without interantennal series.

Terga smooth, polished. Collum broad. Paranota well developed, broadest on anteriormost segments, moderately declined, angling ventrolaterad and continuing slope of dorsum, anterior corners rounded, caudolateral corners variable, either blunt, squared, rounded, or angling caudad. Peritremata distinct; ozopores located caudal to midlength. Caudal segments normal for family.

Sides of metazonites smooth or granular, with or without variable ridges above leg coxae. Strictures broad but distinct. Gonapophyses moderately long and stout, extending moderately from 2nd coxae. Pregonopodal sterna glabrous; 5th sternum with or without low elevations between anterior (4th) legs, with moderate depression between 5th legs; 6th sternum strongly depressed between both legs to accommodate stems of telopodites. Postgonopodal sterna glabrous, unmodified. Coxa and prefemora with or without short projections on certain legs; tarsal claws gently curved. Hypoproct broadly rounded, paraprocts with margins strongly thickened.

Gonopodal aperture ovoid, extending caudad between 9th legs, with or without slight anteriolateral indentations, anterior margin and sides flush with metazonal surface, caudal margin elevated. Gonopods *in situ* with telopodites extending generally forward in subparallel arrangement, overhanging 6th and caudal half of 5th sterna. Coxae moderate-size, with macrosetal tufts above and below cannula, narrowly segregated by narrow sternal band, with either two lateral or one central lobes. Telopodal elements parallel or subparallel for most of lengths, arising basally from prefemur; latter relatively long and slender; prefemoral process narrow and blade-like basally, curving anteriad at midlength to 2/3 length, with or without broad, toothed projection from anterior surface proximal to curve, either expanding distad into deeply divided, bifurcate termination, or blade-like, extending sublinear-

ly and curving apically to subacuminate tip, with or without variable numbers of long, slender barbules scattered along stem distal to midlength curve and clustered apically. Acropodite either acicular, looping over prefemoral process, and without projections, or expanding near midlength and with broad spiniform projection, stem looping thereafter and becoming subacicular. Prostatic groove arising in pit in prefemur, running along medial surface of prefemur onto dorsal or inner surface of acropodite, continuing to terminal opening.

Cyphopodal aperture broad, encircling 2nd legs, sides and caudal margin elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely in aperture, common surface visible in aperture. Valves variable in size, subequal, lightly to moderately hirsute, medial corners gently to strongly extended, subtending slight to moderate central depression. Receptacles moderate-size, alate, with long hairs arising from ventral margin. Operculum moderate-size to large, located lateral to valves.

Distribution—Occurring in the western periphery of the Columbia Plateau Physiographic Province in central Washington and the northern Rocky Mountains and envirous from eastern Washington to western Montana.

Species—Two.

Remarks—I (Shelley 1990) stated that in western Canada, the Xystodesmidae did not occur east of the crest of the Cascade Mountains, although there was an outside possibility that the family might be found around Rossland and Trail where the forests seem more moist and extensive. As *Montaphe* is now known less than 5 mi (8.0 km) south of the International Border in Idaho, it seems certain that this genus is represented in the adjoining part of the interior of British Columbia.

As envisioned here, *Montaphe* is heterogeneous; the only features shared by both component species is the rust color, the narrowly segregated gonocoxae, and the general curvature pattern of the elements of the telopodite. To some degree, *M. paraphoena* represents an abbreviated or shortened version of *M. elrodi*, with the prefemoral process terminating before the acropodal loop rather than after. The acropodite of *M. paraphoena* is much broader and the only one in the tribe with a secondary projection, but I think the general pattern of the gonopodal elements of *M. paraphoena* is similar enough to that of *M. elrodi* to be accommodated at least temporarily under the same genus, as opposed to erecting another monotypic taxon. The two species are roughly 115.5 mi (184.8 km) apart, and the substantial anatomical differences suggest that additional forms may await discovered in central Washington.

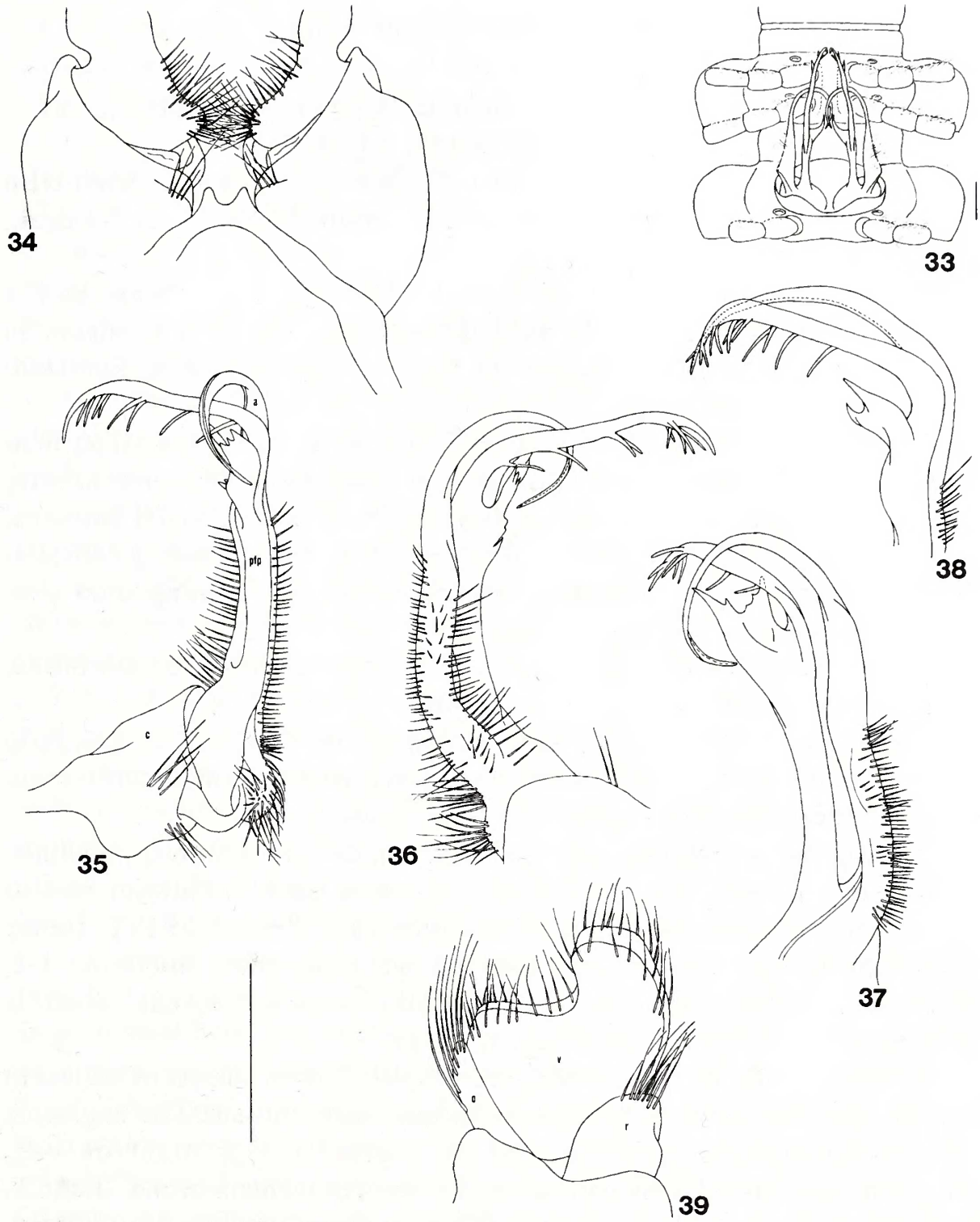


Fig. 33-39. *Montaphe elrodi*. 33, gonopods *in situ*, ventral view of male from Spokane County, Washington. 34, gonocoxae and sternum, caudal view of male syntype. 35, left gonopod of the same, medial view. 36, telopodite of the same, lateral view. 37, the same, subventral view. 38, distal extremity of telopodite of male from Pend Oreille County, Washington, medial view. 39, right cyphopod of female syntype, caudal view. Abbreviations as in Fig. 2-8. Scale line for Fig. 33 = 1.00 mm; line for other Fig. = 1.06 mm for 34 and 36, 1.00 mm for 35 and 37-39.

Montaphe elrodi (Chamberlin)
Figs. 33–39

Leptodesmus (*Chonaphe*) *elrodi* Chamberlin, 1913:424–426, fig. 17.
Amphelictogon elrodi: Attems, 1938:159, fig. 179.
Montaphe elrodi: Chamberlin, 1949:127. Causey, 1954*b*:82. Chamberlin and Hoffman, 1958:38. Loomis and Schmitt, 1971:113–114. Kevan, 1983:2968.

Type specimens—Male lectotype (NMNH) and 9 male and 4 female paralectotypes (MCZ, NMNH) collected by C. C. Adams in the summer of 1912 at an unknown site on Flathead Lake, Flathead/ Lake counties, Montana.

Diagnosis—Prefemoral process long and narrow, blade-like, bent abruptly dorsad near midlength, with broad, irregular, and usually subdivided projection proximal to bend and 5–13 strong, distal barbules; acropodite narrowly blade-like basally, acicular distad, narrowing constantly throughout length, without projections, usually looping over prefemoral process near bend of latter.

Color in life—Paranota rust-colored, metaterga black with broad, rust-colored bands along caudal margins.

Lectotype—Length 27.5 mm, maximum width 4.1 mm, W/L ratio 14.9%, D/W ratio 70.7%. Body essentially parallel sided throughout length, tapering at anterior and posterior ends.

Head capsule smooth, polished; epicranial suture shallow, indistinct. Antennae relatively short and broad, reaching back to anterior part of 4th tergite; relative lengths of antennomeres 2>3=4=5>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial 1-1, interantennal and frontal not detected and presumed absent, genal 1-1, clypeal about 10-10, labral about 12-12.

Collum broad, ends extending slightly below those of adjacent tergite. Paranota well developed throughout body, broadest on segments 1–6, caudolateral corners squared on segments 2–3, blunt on 4–5, rounded on 6–16, angling caudad on 17–18. Peritremata broad, distinct, strongly elevated above paranotal surface; ozopores opening dorsolaterad.

Sides of metazonites smooth, polished. 5th sternum moderately depressed between caudal (5th) legs to accommodate apices of telopodites. Postgonopodal sterna with broad, shallow central impressions and narrow transverse grooves originating between leg pairs, caudal margins gently curved. Coxae and prefemora without projections.

Gonopodal aperture ovoid, 1.7-mm wide and 0.6-mm long at midpoint, without indentations, sides and anterior margin flush with segmental surface, caudal margin strongly elevated into two broadly rounded, caudolateral lobes, lower in midline. Gonopods *in situ* (Fig.

33, not this specimen) with telopodites extending anteriad from aperture and overhanging anterior margin, acropodites curling mediad dorsal to prefemoral processes and overlaying each other in midline, prefemoral processes angling toward each other and extending forward over 6th sternum, apices bent dorsad. Gonopod structure as follows (Figs. 34–37): Coxa moderate size, with macrosetal tufts above and below cannula, narrowly separated from opposite member and connected by narrow sternum, latter with small paramedian lobes subtending coxae. Prefemoral process long and narrow, arising basally on medial side and extending forward in sublinear fashion, with broad, cupulate medial projection at 1/3 length, latter narrow basally then expanding broadly with 5 sharply acute teeth, 2 basally and 3 distad, and a second, more distal projection, also with terminal teeth, arising from the first, stem of prefemoral process bent strongly dorsad at 2/3 length, extending sublinearly and curving downward distad, apically subacuminate, with 8 slender barbules arising from inner margin distal to dorsal bend, spaced more or less equidistantly, clustered at distal curve. Acropodite arising lateral to prefemur, long, slender, and acicular, looping over prefemoral process at level of caudal bend, curling over medial surface of latter and overhanging medial projection, apically acuminate.

Male paralectotypes—The medial projection of the prefemoral process varies with more or fewer teeth than in the lectotype. The number of barbules varies from 5–13, which are generally clustered distad near the distal curve and evenly spaced back to the bend at 2/3 length. One paralectotype has a barbule proximal to the bend.

Female paralectotype—Length 23.6 mm, maximum width 4.5 mm, W/L ratio 19.1%, D/W ratio 80.0%. Agreeing closely with lectotype in structural details except paranota slightly shorter and more declined, creating appearance of more vaulted body. Valves (Fig. 39) moderately large and subequal, moderately hirsute, medial corners extending ventrad well below level of lateral corners, subtending central cavity. Receptacle relatively small, alate, cupped below medial corner of valves, extending slightly up anterior and caudal surfaces of latter, with long hairs arising from ventral margins. Operculum large, located laterad to valves.

Variation—As in the paralectotypes, variation among nontypical males primarily involves the configuration of the medial projection of the prefemoral process and the number and arrangements of barbules. The medial projection is flattened and plate-like in some males, while it is lobate in others; in the western part of the range its margins are smoother and less serrate than in the types (Fig. 38). The barbules vary as in the paralectotypes, clustering distad, being rather evenly spaced proximad, and typically arising distal to the bend at 2/3 length.

Additionally, the acropodite occasionally does not loop over the prefemoral process, but lies roughly parallel to it (Fig. 38).

Ecology—According to labels with preserved samples, *M. elrodi* has been encountered in a field under stones and logs, under rocks, and in moss near a small woodland stream. The specimens that I collected in Boundary and Bonner counties, Idaho, were found in moist deciduous litter in hardwood patches in predominantly coniferous forests; those from Idaho County were taken from litter in a ditch beside a walkway in a large area of deciduous trees; and that from Pend Oreille County, Washington, was encountered under a log and rock on a talus slope in a cool, moist cove along a stream. Loomis and Schmitt (1971) encountered the milliped between and under rocks, moss, logs, cedar bark, in rotten wood, between rocks just above the splash zone of cascading water in a stream, at the base of a talus slide, and in a red cedar, Douglas-fir forest. Sites were typically in creek bottoms with thick humus layers, and a number of specimens were taken in cedar groves.

Distribution—Spokane and Stevens counties, Washington, to Lake County, Montana, and from just south of the International Border in Boundary County, Idaho, and Pend Oreille County, Washington, to northern Idaho County, Idaho, north of the transverse stretch of the Salmon River. The area is approximately 242 mi (387 km) in the east-west dimension and 216 mi (346 km) in the north-south. The Whitman County, Washington, record is from the Columbia Plateau, and most of the other sites are in the Northern Rocky Mountains Physiographic Province. Specimens were examined as follows:

WASHINGTON: *Pend Oreille Co.*, ca. 4 mi (6.4 km) N Metaline Falls, along feeder stream to Sullivan Cr., ca. 1.7 mi (2.7 km) E WA hwy. 31, M, 31 May 1993, R. M. Shelley (NCSM); ca. 9 mi (14.4 km) SSE Metaline Falls, Noisey Cr. Cpgd., Sullivan L., 2M, 2F, 10 July 1988, R. W. Baumann, Wells, Whiting (BYU); and Gypsy Meadow NE Metaline Falls, 48.903°N, 117.080°W, F, 13 June 1986, R. Crawford (UWBM). *Spokane Co.*, Four Lakes, Granite L., 3M, F, 30 May 1947, M. H. Hatch (FSCA); Mt. Spokane St. Pk., Deadman Cr., F, 10 July 1988, R. W. Baumann, Wells, Whiting (BYU); and Spokane, M, F, 22 July 1882, S. Henshaw (MCZ). *Whitman Co.*, Ewan, 3M, F, 27 August 1932, M. H. Hatch (FSCA, UWBM).

IDAHO: *Boundary Co.*, 4 mi (6.4 km) SW Porthill, along Canyon Cr., 2M, 3F, 12 August 1991, R. M. Shelley (NCSM). *Bonner Co.*, 7.5 mi (12.0 km) N Priest River, along ID hwy. 57, M, F, 11 August 1991, R. M. Shelley (NCSM). *Shoshone Co.*, N Kellogg, 1.3 mi (2.0

km) up Steamboat Cr. from Coeur d'Alene R., 8M, 3F, 15 May 1975, F. W. Grimm (CMN). *Clearwater Co.*, 5.2 mi (8.3 km) N, 0.5 mi (0.8 km) E Headquarters, 4M, 9 July 1978, A. K. Johnson (NCSM); and 8.7 mi. (13.9 km) E, 5.7 mi. (8.0 km) N Pierce, French Mtn. Rd., 19M, 17F, 2 and 4 July 1978, A. K. Johnson (NCSM). *Idaho Co.*, 13 mi (20.8 km) SSE Pierce, Eldorado Ridge, M, 12 July 1978, A. K. Johnson (NCSM); 4 mi (6.4 km) SW Lolo Pass, US hwy. 12 at Russian Cr., 11M, 11F, 3 September 1978, A. K. Johnson (NCSM); 11 mi (17.6 km) SW Lolo Pass, along US hwy. 12, M, 25 June 1968, G. B. Wiggins, Yamamoto, Smith (ROM); 24.3 mi (38.9 km) E Lowell, along US hwy. 12, 3M, 3F, 10 June 1981, R. M. and S. B. Shelley, P. D. Hardister (NCSM); Lowell, M, 2F, 4 July 1949, C. O. Bowles, (NMNH); 1.1 mi (1.8 km) S Stites, Nez Perce Ind. Res., M, 15 May 1975, F. W. Grimm (CMNH); and 3 mi (4.8 km) E Syringa, Middle Fork Clearwater R., 2M, F, 15 May 1975, F. W. Grimm (CMN).

MONTANA: *Sanders Co.*, 1 mi (1.6 km) W Noxon, 3M, 4F, 2 May 1965, R. Schmitt (FSCA). *Missoula Co.*, Clinton, Hell Gate Run, 3M, 3F, August 1930, collector unknown (NMNH). *Flathead Co.*, Big Fork, M, F, 24 August 1957, H. W. and L. L. Levi (MCZ). *Flathead/ Lake cos.*, along Flathead L., 4M, F, 22 June 1909, collector unknown (EIL); and Flathead L., 10M, 4F, summer 1912, C. C. Adams (MCZ, NMNH) TYPE LOCALITY. *Lake Co.*, 6 mi (9.6 km) E St. Ignatius, Mission Cr. Canyon, 4M, 3F, 2 September 1978, A. K. Johnson (NCSM).

The following additional literature records are considered valid and are denoted by open symbols in figure 68. Those from Idaho and Montana are by Loomis and Schmitt (1971).

WASHINGTON: *Stevens Co.*, Evans (Causey 1954*b*).

IDAHO: *Idaho Co.*, 3.1 mi (5.0 km) W Surveyor Cr.

MONTANA: *Lake Co.*, along Big Fork River and North Crow, Dog, Jocko, Schmidt, and Hell Roaring Creeks; canyon near Mission Falls; St. Ignatius and 4.0 mi (6.4 km) E St. Ignatius; 8.5 mi (13.6 km) SE Swan Lake guard station; along Goat Cr., 10.0 mi (16.0 km) S Swan Lake; along Big Knife Cr., 5.0 mi (8.0 km) from Arlee; Methodist Camp, Rollins; McDonald Peak; Mission and McDonald cirques; Lake Mary Ronan; and Yellow Bay. *Missoula Co.*, along Smith Cr. near Condon ranger station; 1.0 mi (1.6 km) below Smith Cr.; along Crazy Horse Cr.; Pattee Cyn. Rec. Area; along Miller Cr. and Mt. Sentinel, Missoula; and along Nine Mile Cr., Huson.

Remarks—The black base color of *M. elrodi* is restricted to the prozonum and a narrow area on the anterior edge of the metaterga, so the rust-colored bands cover most of the latter and dominate the milliped's appearance. At first glance, it appears almost uniformly rust colored.

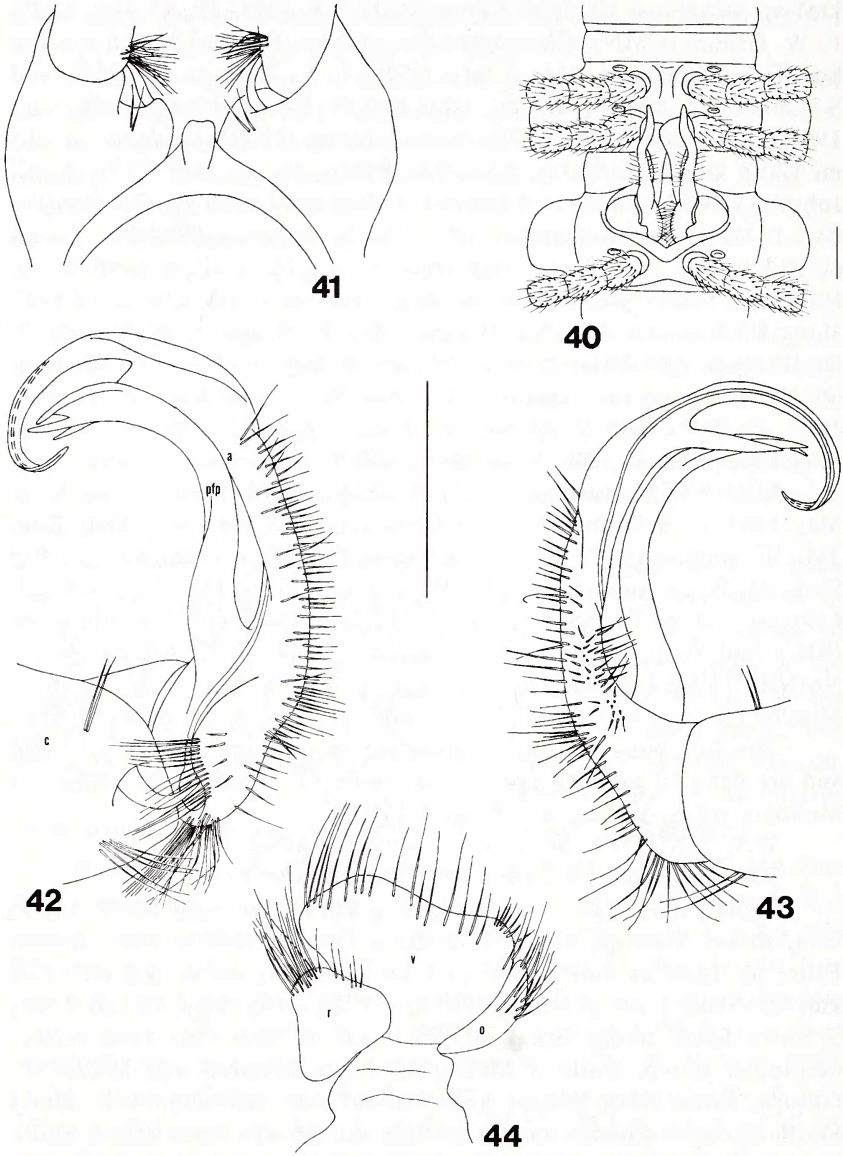


Fig. 40-44. *Montaphe paraphoena*. 40, gonopods *in situ*, ventral view of paratype. 41, gonocoxae and sternum, caudal view of paratype. 42, left gonopod of holotype, medial view. 43, the same, lateral view. 44, left cyphopod of female paratype, caudal view. Abbreviations as in Figs. 2-8. Scale line for Fig. 40 = 1.00 mm; line for other Figs. = 3.20 mm for 41, 2.22 mm for 42-43, 1.00 mm for 44.

In August 1991 I visited Glacier National Park and searched for *M. elrodi* at lower elevations on the west side of the Park, near Apgar, McDonald Lake, and the cedar grove near Avalanche Campground. As with Loomis and Schmitt (1971), I did not encounter *M. elrodi* in these areas or in regions outside the Park near Whitefish, Columbia Falls, and Hungry Horse Reservoir. The species therefore seems to be absent from areas north/northeast of Flathead Lake.

Montaphe elrodi is the dominant species in the eastward xystodesmid faunal extension into western Montana. Extremely abundant between eastern Washington and Flathead Lake, *M. elrodi* is now known from about 3 mi (4.8 km) south of the International Border near Porthill, Boundary County, Idaho, and should therefore be expected near Creston, British Columbia, only about 7 mi (11.2 km) north of Porthill. Records from Metaline Falls, Pend Oreille County, and Evans, Stevens County, Washington, are only about 10 and 20 mi (16 and 32 km) south of the border and suggest the occurrence of *M. elrodi* near Walneta and Nelway, British Columbia. It may also occur near Rossland and Trail, although they are just west of the Columbia River, which may constitute a distributional barrier. When collected, *M. elrodi* will represent a new genus and species for Canada.

Montaphe paraphoena, new species

Figs. 40–44

Type specimens—Male holotype and 13 male, 6 female, and 1 juvenile paratypes (UWBM) collected by R. Crawford, K. Dorweiler, and J. P. Pelham, 27 April 1991, in Tichenal Canyon, 7.5 mi (12.0 km) south, 1.5 mi (2.4 km) east of Waterville, (47.540°N, 120.035°W), Douglas County, Washington. One male and one female paratypes deposited in the NCSM.

Diagnosis—Prefemoral process short, expanding distad to irregular, deeply divided, bi-lobed termination within curvature of acropodite; latter expanding basically with thickened medial margin and spiniform lateral projection, narrowing thereafter, becoming subacicular apically.

Color in life—Paranota rust-colored, metaterga black with broad, rust-colored bands along caudal metatergal margins.

Holotype—Length 23.6 mm, maximum width 4.1 mm, W/L ratio 17.4%, D/W ratio 78.0%.

Somatic features agreeing with those of *M. elrodi*, with following exceptions:

Epicranial suture distinct, accentuated by narrow black line. Width across genal apices 2.6 mm, interantennal isthmus 0.9 mm. Relative lengths of antennomeres 2>3>6>4>5>1>7. Genae with distinct central

impressions. Facial setae as follows: epicranial 2-2, interantennal not detected and presumed absent, subantennal 1-1, frontal 1-1, genal 4-4, clypeal about 30-30, labral about 16-16.

Sides of metazonites granular, with ventral ridges just above leg coxae on segments 1–14, higher and more distinctly elevated above metazonal surface on segments 1–4, becoming progressively lower caudad. 5th sternum with two low, widely segregated, paramedian knobs between anterior (4th) legs, shorter than widths of adjacent coxae, and moderate depression between 5th legs. Coxae with small medial lobes on legs 3–5; prefemora with short, indistinct ventrodistal spines on legs on segments 10–16.

Gonopodal aperture generally ovoid, extending slightly caudad between 9th legs, 1.6-mm wide and 0.9-mm long at midpoint, indented slightly anteriolaterad, anterior margin and sides flush with metazonal surface, caudal margin becoming elevated at caudolateral corner, rising slightly to midline. Gonopods *in situ* (Fig. 40, of paratype) with telopodites extending generally anteriad from aperture and overhanging 6th sternum, acropodites and prefemoral processes angling toward each other and overlapping in midline. Gonopod structure as follows (Figs. 41–43). Coxa moderately large, with 2 dorsal and 4 ventral macrosetae, narrowly segregated from opposite member by narrow sternal band, latter with medial lobe. Prefemoral process short and broad, arising from dorsal surface, curving broadly at 2/3 length and expanding distad, deeply divided apically and terminating inside loop of acropodite in two acuminate determinations, medial one broader. Acropodite arising ventrad on prefemur, curving over prefemoral process in subparallel arrangement, expanding broadly with thickened medial margin and with strong projection from lateral surface distal to midlength, latter spiniform, extending nearly to level of terminus of prefemoral process, stem of acropodite narrowing slightly distad and looping dorsad beyond terminus of prefemoral process, curling to acuminate tip.

Male paratypes—The male paratypes agree with the holotype in all particulars.

Female paratype—Length 25.6 mm, maximum width 4.0 mm, W/L ratio 15.6%, D/W ratio 87.5%. Agreeing essentially with the males in somatic features except paranota more strongly declined, creating appearance of more vaulted body. Valves (Fig. 44) small, subequal, lightly hirsute, becoming slightly higher mediad but without distinct lobes or projections, slightly depressed centrally. Receptacle small, alate, cupped around medial side of valves, with long hairs arising from outer surface. Operculum relatively large, located laterad to valves.

Ecology—The types were found under rocks on soil on a barren slope in a heavily grazed, grassland area.

Distribution—Known only from the type locality, which is on the eastern side of Badger Mountain and in the western periphery of the Columbia Plateau Physiographic Province.

Genus *Tubaphe* Causey

Tubaphe Causey, 1954*a*:222. Chamberlin and Hoffman, 1958:52. Jeekel, 1971:291. Hoffman, 1979:159. Kevan, 1983:2968.

Type species—*Tubaphe levii* Causey, 1954, by original designation.

Diagnosis—Paranota present only on segments 1–4, remaining segments appearing nearly juloid, with at most only slight ozopore swellings; epiproct with distal constriction; gonocoxae narrowly segregated, attached by membrane only, without trace of sclerotized band; telopodal elements diverging, not parallel, prefemoral process arising near midlength of prefemur, acropodite arising distad; prefemoral process subacicular, gently curved, with minute distal barbules; acropodite narrowly blade-like to subacicular, in form of broad, open loop curving through a single vertical plane; cyphopod valves with medial corners projecting distinctly ventrad, subtending central cavity.

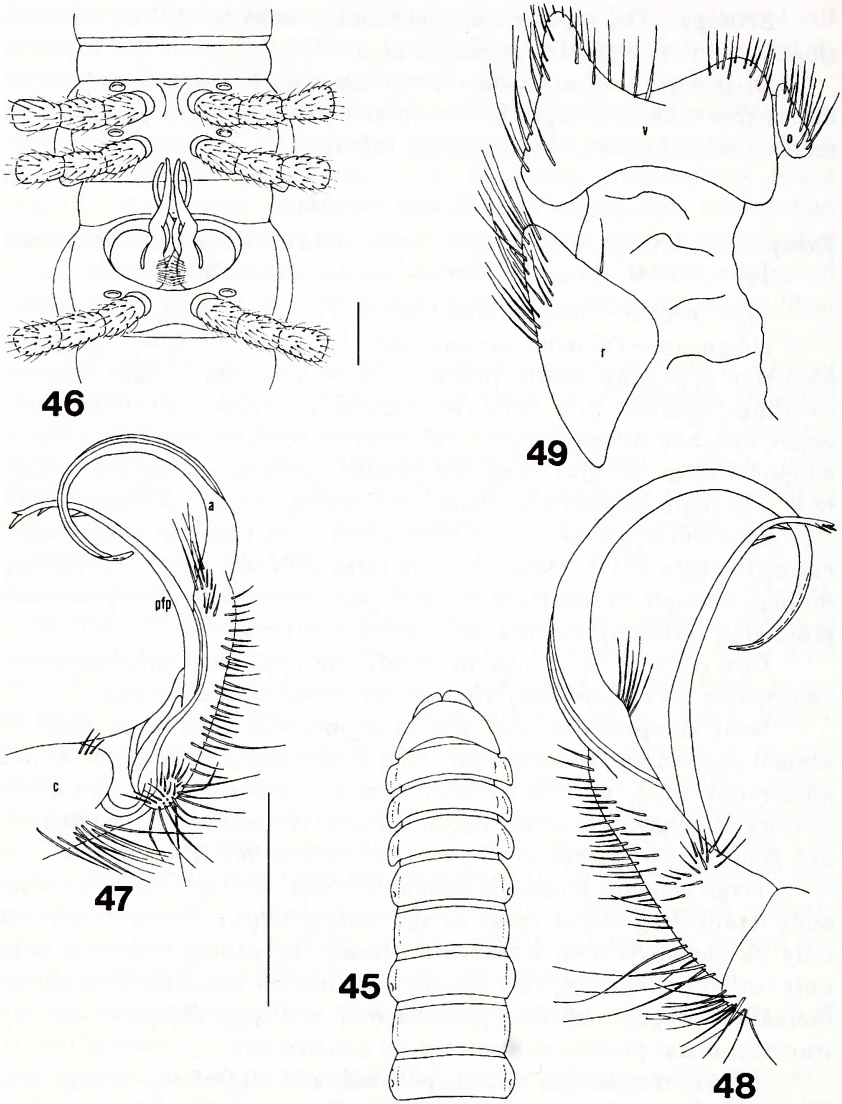
Description—A genus of small, narrow, and subcylindrical chonaphine Xystodesminae with the following characteristics.

Body composed of head and 20 segments in both sexes. Head of normal appearance, smooth. Epicranial suture sharp, distinct. Antennae moderately long, with 4 conical, terminal sensory cones, no other sensory structures apparent. Facial setae with epicranial, subantennal, and genal series present or absent, with clypeal and labral series.

Terga smooth, polished; strictures broad, distinct. Collum broad, ends terminating above those of succeeding tergite. Paranota present only on segments 1–4, strongly declined, succeeding segments with only ozopore swellings. Peritremata indistinct on segments 2–4, absent thereafter; ozopores opening sublaterad on swellings. Epiproct apically truncate, distal portion demarcated by constriction.

Sides of metazonites smooth, polished, with slight lobes on segments 2–4. Pregonopodal sterna glabrous, without modifications, strongly depressed on segment 6. Postgonopodal sterna glabrous, flat, and unmodified, with only shallow transverse grooves originating between leg pairs. Coxae with short tubercles on legs of segments 7–14; prefemora with ventrodistal spines on legs of segments 9–18.

Gonopodal aperture ovoid, without caudal extension. Gonopods *in situ* with telopodites in parallel arrangement. Coxae with macrosetae varying from 2–10 in two tufts, above and below cannula, attached by



Figs. 45-49. *Tubaphe levii*. 45, profile of anterior segments of male from Jefferson County, Washington, dorsal view. 46, gonopods *in situ*, ventral view of male from Vancouver Island, British Columbia. 47, left gonopod of male from Jefferson County, Washington, medial view. 48, telopodite of the same, lateral view. 49, left cyphopod of female from Jefferson County, caudal view. Abbreviations as in Figs. 2-8. Scale line for Fig. 46 = 1.00 mm; line for other Figs. = 0.5 mm for 45, 1.00 mm for 47-48, 1.30 mm for 49.

membrane only, without trace of sternal band. Telopodal elements diverging, not parallel; prefemur long and narrow; prefemoral process arising near midlength of prefemur, long, narrow, and subacicular, gently curved, extending beyond level of distal extremity of acropodal curvature, with 3–4 minute, distal barbules. Acropodite arising distad on prefemur, long and narrow, blade-like to subacicular, demarcated from prefemur by narrow constriction, configuration a broad, open loop curving over prefemoral process to acuminate tip. Prostatic groove arising in pit on prefemur, angling to lateral side of prefemur and extending onto base of acropodite, continuing to terminal opening.

Cyphopod aperture relatively narrow, encircling 2nd legs, sides and caudal margin elevated above metazonal surface. Cyphopods in situ with valves oriented transversely, common surface visible in aperture. Valves relatively large, subequal, and lightly hirsute, medial corners extending strongly ventrad, subtending deep central cavity. Receptable moderate-size, subtriangular, located below medial corners of valves, not cupped around latter, with numerous long hairs. Operculum large, located lateral to valves, with numerous long hairs.

Distribution—Along the Pacific Coast on the southwestern periphery of Vancouver Island, British Columbia, and on the western and southwestern slopes of the Olympic Mountains, Washington.

Species—One.

Tubaphe levii Causey

Figs. 45–49

Tubaphe levii Causey, 1954*a*:223, figs. 2–4. Chamberlin and Hoffman, 1958:52. Kevan, 1983:2968.

Metaxycheir pacifica Shelley, 1990:2311–2313, figs. 1–5.

Type specimens—Male holotype (AMNH) and 2 female paratypes (FSCA) collected by H. W. and L. L. Levi, 12 July 1951, at Graves Creek Campground, Olympic National Park, Jefferson County, Washington. One gonopod of the holotype is lost and the other is broken.

Diagnosis—With the characters of the genus, as illustrated in figures 45–49.

Description—Recently collected males from Jefferson County, Washington, conform closely to the detailed anatomical account by Shelley (1990) of the synonym, *M. pacifica*; the following supplemental observations are the only significant additions.

Facial setae: epicranial generally not detected and presumed absent; one male with one seta per side. Subantennal 1–1 and genal 2–2 on most males.

The gonocoxae are loosely joined by membrane with no trace of a sternal remnant. The coxal macrosetae are in two clusters, one above, and one below, the cannula, and vary in numbers from 2 to a cluster of 8–10.

Ecology—In Washington, *T. levii* is restricted to the wet rain forests on the western and southwestern slopes of the Olympic Mountains. I did not encounter the milliped in the wettest areas during my 1990 field trip, for example around the Hoh Visitor Center, Olympic National Park, because the vegetation is so dense that there are few areas with exposed litter. My success came in slightly drier areas, where *T. levii* was typically encountered in association with decaying deciduous logs, usually under bark. This contrasts with the situation on Vancouver Island, where I found the milliped in deciduous leaf litter in August 1989 (Shelley 1990).

Distribution—The western periphery of Vancouver Island, Canada, from the vicinities of Bamfield to China Beach Provincial Park up to 3–6 mi (5–10 km) inland, and western Clallam, and western and southern Jefferson, counties, Washington, from Bogachiel State Park to Graves Creek Campground, Olympic National Park. Canadian localities are detailed in Shelley (1990); American localities are as follows:

WASHINGTON: *Clallam Co.*, Bogachiel St. Pk., M, 6F, 23 August 1990, R. M. Shelley (NCSM). *Jefferson Co.*, Hoh rain forest, Olympic Nat. Pk., M, F, 5 May 1991, K. A. Buhlmann (VMNH); along Hoh River Rd. just outside boundry of Olympic Nat. Pk., ca. 7.4 mi (11.8 km) E jct. US hwy. 101, 3M, 4F, 24 August 1990, R. M. Shelley (NCSM); along Queets River Rd., Olympic Nat. Pk., 0.6 mi (0.9 km) inside park boundary, M, 4F, 2 juvs., 24 August 1990, R. M. Shelley (NCSM) and 4.8 mi (7.7 km) inside park boundary, M, F, 24 August 1990, R. M. Shelley (NCSM); and Graves Cr. Cpgd., Olympic Nat. Pk., M, F, 12 July 1951, H. W. & L. L. Levi (AMNH, FSCA) TYPE LOCALITY.

Remarks—Among American xystodesmids, the absence of paranota and the cylindrical, nearly julidan body form caudal to segment 4 is unique to *T. levii*. There are species in which the paranota are reduced and thus appear somewhat cylindrical, for example *S. placidus*, but no others in which these structures are entirely absent. Consequently, *T. levii* probably occupies a distinct ecological niche apart from that of the sympatric xystodesmid *Harpaphe h. haydeniana* (Wood). It is noteworthy that there is much greater variation in body form among the western, or western-related, xystodesmids than in the eastern tribes, for in addition to the cylindrical and subcylindrical *T. levii* and *S. placidus*, there are two highly convex species, *Isaphe convexa* Cook

and *Thrinaphe hargeri* Shelley (Shelley 1993*c*, *d*), and the extremely flat species of *Sigmocheir* in the Sierra Nevada Mountains of California. In contrast, although the eastern forms, representatives of the tribes Apheloriini, Rhysodesmini, Nannariini, and Pachydesmini, differ in the degree of convexity, they demonstrate similar overall body forms without nearly the somatic differences of the western species. Adaptive radiation of western xystodesmids has manifested itself in general body form to a much greater degree than has that of the eastern fauna.

Genus *Metaxycheir* Buckett and Gardner

Metaxycheir Buckett and Gardner, 1969:67. Hoffman, 1979:157. Kevan, 1983:2968.

Type species—Metaxycheir prolata Buckett and Gardner, 1969, by original designation.

Diagnosis—Paranota present and distinct on all segments; epiproct without constriction; gonocoxae narrowly segregated by narrow sternal band, latter with central lobe; telopodal elements not parallel, prefemoral process arising near midlength of prefemur, acropodite arising distad; prefemoral process narrowly blade-like, slightly bisinuate, without projections; acropodite narrowly blade-like, in form of narrow, open loop, curving through more than one vertical plane; cyphopod structure unknown.

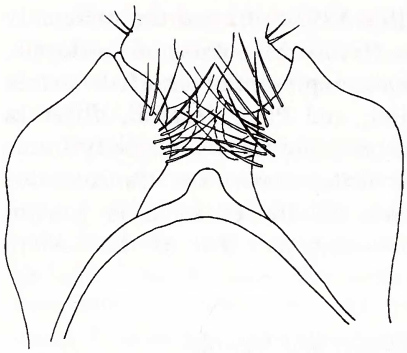
Description—A genus of small to moderate-size chonaphine xystodesminae with the following characteristics:

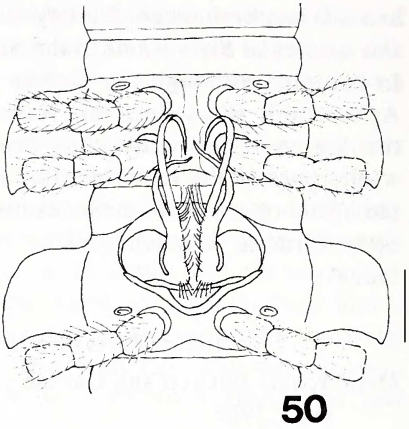
Body composed of head and 20 segments in both sexes. Head of normal appearance, smooth. Epicranial suture sharp, distinct. Antennae moderately long, with 4 conical, terminal, sensory cones and microsensilla on penultimate antennomeres. Facial setae with epicranial, interantennal, frontal, genal, clypeal, and labral series; genal setae arranged among 3 groups.

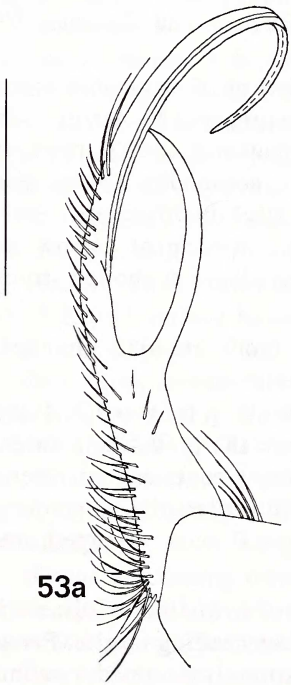
Terga smooth, polished; strictures broad, distinct. Collum large and broad, ends terminating above those of succeeding tergite. Paranota present on all tergites, broadest anteriorly, strongly declined, continuing slope of dorsum and creating appearance of vaulted body. Peritremata moderately distinct; ozopores opening sublaterad.

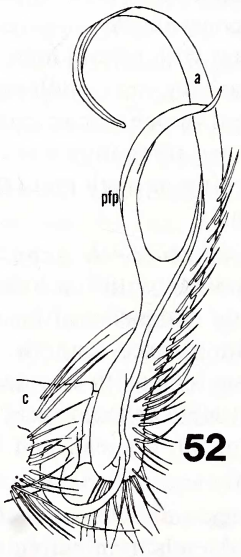
Caudal segments normal for family.

Sides of metazonites smooth, polished. Pregopnopodal sterna of males with small lobes between anterior legs of 5th segment (4th legs), moderate depression between 5th legs; 6th sternum strongly depressed between both legs. Postgonopodal sterna flat, glabrous, and









Figs. 50-53a. *Metaxycheir prolata*. 50, gonopods *in situ*, ventral view of male from Latah County, Idaho. 51, gonocoxae and sternum of male from Benewah County, Idaho, caudal view. 52, left gonopod of the same, medial view. 53a, telopodite of the same, lateral view. Abbreviations as in Figs. 2-8. Scale line for Fig. 50 = 1.00 mm; line for other Figs. = 1.20 mm for 51, 1.00 mm for 52-53.

unmodified, with only shallow transverse grooves originating between leg pairs. Coxae of legs 3-7 moderately enlarged ventrad, swelling of 3rd coxae angular on anterior surface; prefemora without trace of spines.

Gonpodal aperture generally ovoid, with caudal extension between 9th legs. Gonopods *in situ* with telopodites in parallel arrangement. Coxae with macrosetae fields in two general tufts, attached to each other by narrow sternal band, latter with central lobe. Telopodal elements not parallel; prefemur long and narrow; prefemoral process arising near midlength of prefemur, narrowly blade-like, apically acuminate, bisinuately curved, without projections. Acropodite arising distad from prefemur, long and blade-like, curving in form of narrow arc, acuminate. Prostatic groove arising in pit in prefemur, running along medial face of prefemur, angling onto lateral surface of acropodite and continuing to terminal opening.

Females unknown.

Distribution—Whitman County, Washington, to Benewah and Latah counties, Idaho.

Species—One.

Remarks—Among the three genera with long prefemoral processes, *Metaxycheir* has the simplest gonopod, consisting of an unmodified blade-like prefemoral process and a blade-like acropodite. I show them as an unresolved trichotomy in figure 72, but *Metaxycheir* may be the sister lineage to *Tubaphe* + *Montaphe*.

Metaxycheir prolata Buckett and Gardner

Figs. 50–53a

Metaxycheir prolata Buckett and Gardner, 1969:67–70, figs. 1–6. Kevan, 1983:2968.

Type specimen—Male holotype and 2 juvenile paratypes (UCD) collected by R. L. Westcott, 16 May 1965, 7 mi (11.2 km) NE Moscow, Latah County, Idaho. The vial label and citation in Buckett and Gardner (1969) incorrectly state Nez Perce County, but this site is actually in Latah County.

Diagnosis—With the characters of the genus.

Color in life—Unknown; the specimens that I collected in Whitman County, Washington, were freshly molted and lacked pigmentation.

Male from Benewah County, Idaho—The following notes on somatic features supplement the complete characterization of the holotype by Buckett and Gardner (1969); for consistency in terminology with previous accounts, gonopodal features are described in detail.

Length 20.4 mm, maximum width 3.6 mm, W/L ratio 17.6%, D/W ratio 75.0%.

Width across genal apices 2.1 mm, interantennal isthmus 0.7 mm. 6th antennomere with minute distal microsensilla. Facial setae as follows: epicranial 2-2, interantennal 1-1, frontal 2-2; genal with four groups, a central group of 4-4, one lateral to this of 1-1, one beneath antennae of 1-1, and one submarginal of 4-4; clypeal about 24-24; labral about 18-18.

Dorsum smooth, polished. Paranota well developed throughout body, broadest on anterior segments, strongly declined, angling sharply ventrad and creating appearance of strongly convex body, anterior corners rounded on all segments, caudolateral corners blunt on segments 1–4, produced slightly caudad beginning on 7 and continuing thusly to caudal end of body. Peritremata moderately distinct, moderately elevated above paranotal surface; ozopores located caudal to midlength, opening sublaterad.

Sides of metazonites smooth, polished. Gonapophyses short and broad, only slightly extending from 2nd coxae. 5th sternum with 2 short projections subtending 4th coxae, moderately depressed between 5th legs; 6th sternum strongly depressed between both leg pairs to accommodate stems of telopodites. Coxae of legs 3–7 swollen ventrad, remaining coxae unmodified, prefemora without projections.

Gonopodal aperture ovoid, extending strongly caudad between 9th legs with shelf in extension, 1.8-mm wide and 0.8-mm long at midpoint, without indentations, anterior margin flush with metazonal surface, sides elevating strongly caudad to caudolateral corner, dropping slightly on caudal extension but still well elevated above metazonal surface. Gonopods *in situ* (Fig. 50) with telopodites extending anteriad in parallel arrangement over 6th sternum, prefemoral processes curving toward each other and nearly meeting in midline. Gonopod structure as follows (Figs. 51–53a): Coxa moderate size, with sublinear field of 8–10 macrosetae, connected to opposite member by moderately sclerotized sternum, latter with medial lobe. Prefemoral process long, narrowly blade-like, arising anteriolaterad on prefemur, curving broadly mediad basally then anteriad in generally bisinuate appearance, apically acuminate. Acropodite blade-like, curving broadly anteriad then dorsad distally, sides narrowing gradually to acuminate tip, forming narrow loop.

Ecology—The Whitman County, Washington, specimens were found under thin layers of moist leaves on relatively hard substrate in a deciduous thicket beside the picnic area at Steptoe Butte. According

to the vial label, the Benewah County, Idaho, specimen was collected from under cow dung.

Distribution—Same as that of the genus, a small area of about 25.1 mi (40.2 km) east/west and 16.9 mi (27.0 km) north/south. Specimens were examined as follows:

WASHINGTON: *Whitman Co.*, Steptoe Butte, M, 2F, juv., 3 June 1993, R. M. Shelley (NCSM).

IDAHO: *Benewah Co.*, 4.0 mi (6.4 km) SE Emida, M, 16 April 1987, R. S. Zack (WSU). *Latah Co.*, 7.0 mi (11.2 km) NE Moscow, M, 2 juvs., 16 May 1965, R. L. Westcott (UCD) TYPE LOCALITY; and 3.0 mi (4.8 km) SE Harvard, Laird Park, M, 1 May 1971, W. A. Turner (WSU).

Remarks—No females have been collected of *M. prolata*, so the cyphopod structure is unknown.

This species has a much broader, less acicular and more blade-like, acropodite than do the other chonaphine species with long prefemoral processes. However, the aperture and sternum conform to those of the species of *Chonaphe*, *Montaphe*, and *Semionellus*.

Selenocheir, new genus

Type species—*Selenocheir sinuata*, new species.

Diagnosis—Paranota present and variably distinct on all segments; epiproct without constriction; gonocoxae moderately separated, attached by membrane only, without trace of sclerotized band; telopodal elements not parallel, prefemoral process arising proximad on prefemur, acropodite arising distad; prefemoral process short, less than half as long as acropodite, generally sublinear, apically variable; acropodite variably blade-like to subacicular, subtending broad, variable arc, curving through single vertical plane; cyphopod valves without lobes, extensions, or cavities; receptacle very large, partly enveloping valves.

Description—A genus of moderately large chonaphine Xystodesminae with the following characteristics.

Body composed of head and 20 segments in both sexes, essentially parallel sided, tapering at both ends.

Head of normal appearance, smooth, polished. Epicranial suture distinct, terminating in interantennal region. Antennae relatively long and broad, becoming progressively more hirsute distad, with 4 conical sensory cones and microsensilla on outer distal margin of penultimate antennomere. Genae not margined laterally, with shallow central impressions, ends narrowly rounded and extending just beyond adjacent cranial margins. Facial setae with epicranial, genal, clypeal, and labral series present, with or without interantennal, subantennal, and frontal series.

Terga smooth, polished. Collum relatively broad, ends terminating below or at same level as those of following tergite. Paranota well developed, broadest on anteriormost segments, moderately declined, continuing slope of dorsum, anterior corners with variably small denticles on segments 2–4, rounded thereafter, caudolateral corners variable, either angular, blunt, or rounded. Peritremata broad, moderately distinct, moderately elevated above paranotal surface; ozopores located caudal to midlength, opening laterad to sublaterad. Caudal segments normal for family.

Sides of metazonites with irregularly serrate to jagged ridges subtending leg coxae in anteior half of body. Strictures distinct. Gonapophyses moderately long, extending moderately from 2nd coxae. Pregonopodal sterna glabrous; 4th sternum unmodified; 5th sternum with variable low knobs or elevated areas between 4th legs, flat, depressed, or with low, elevated areas between 5th; 6th sternum either depressed between both legs or with widely separated lobes between anterior pair. Postgonopodal sterna glabrous, unmodified, with at most only shallow transverse grooves, caudal margins smooth and gently curved. Coxae without projections; prefemora with variably short, indistinct ventrodistal spines in caudal half of body; tarsal claws gently curved. Hypoproct broadly rounded, usually slightly extended in midline; paraprocts with margins strongly thickened.

Gonopodal aperture generally broadly ovoid, with at most only very slight caudal extension of caudal margin, without anteriolateral indentations, anterior margin flush with metazonal surface, sides elevating caudad and continuing onto caudal margin, latter flared. Gonopods *in situ* with telopodites directed either anteriad or anteromediad from aperture, angling toward each other, lying parallel or crossing in midline, extending forward over anterior margin of aperture and 6th sternum. Coxae moderate-size, with 2 macrosetae above cannula and variably dense cluster below, connected by membrane only, without trace of sclerotized sternal band. Telopodal elements not parallel; prefemur relatively short to moderately long; prefemoral process short, arising proximad on anterior side, latter less than half as long as acropodite, generally sublinear basally, with or without slight curve or bend at midlength, apically broad or narrow, variably divided or simple. Acropodite arising distad from prefemur, either smoothly or demarcated by constriction, directed anteriad or anteromediad, relatively long, blade-like basally, narrowing distad and in some cases becoming subacicular, curving downward or dorsad distally and subtending variable arch, with or without variably sinuate to uncinate apical bends or curves, apically acuminate. Prostatic groove arising in pit in prefemur, running

along medial surface of latter and crossing to lateral side at base of acropodite, crossing back to inner surface, or continuing along outer, to terminal opening.

Cyphopodal aperture broad, encircling 2nd legs, sides and caudal margin elevated above metazonal surface, latter rising to peak in midline. Cyphopods *in situ* with valves oriented transversely in aperture, common surface visible in opening. Valves variable in size, subequal or anterior valve slightly larger, without distinct lobes or cavities, situated nearly entirely on top of (ventral to) receptacle. Latter large, alate, cupped around valves, more so on anterior side, with long hairs arising from ventral margin. Operculum small to large, located laterad to valves, with numerous long hairs.

Distribution—From Curry and Jackson counties, in southwestern Oregon, to Mendocino and El Dorado counties, California, in the northern Coast Range, the northern Sacramento Valley, and the Sierra Nevada foothills, an area of about 176 mi (282 km) east/west and 273 mi (437 km) north/south.

Species—Three are currently recognized.

Remarks—The Chonaphini is the best placement for this genus, as the only other option is a new tribe. It displays narrowly blade-like to acicular acropodites that are similar to those of *Tubaphe* and *Metaxycheir*, and shares the absence of a sternum with *Tubaphe*. The short prefemoral process is plesiomorphic, and *Selenocheir* tends to bridge the anatomical gap between the Chonaphini and Harpaphini in having a larger coxa in relation to the overall bulk of the telopodite, and in the anteromedially directed acropodites, particularly in *S. directa*, reminiscent of the condition in *Isaphe* (Shelley 1993*d*).

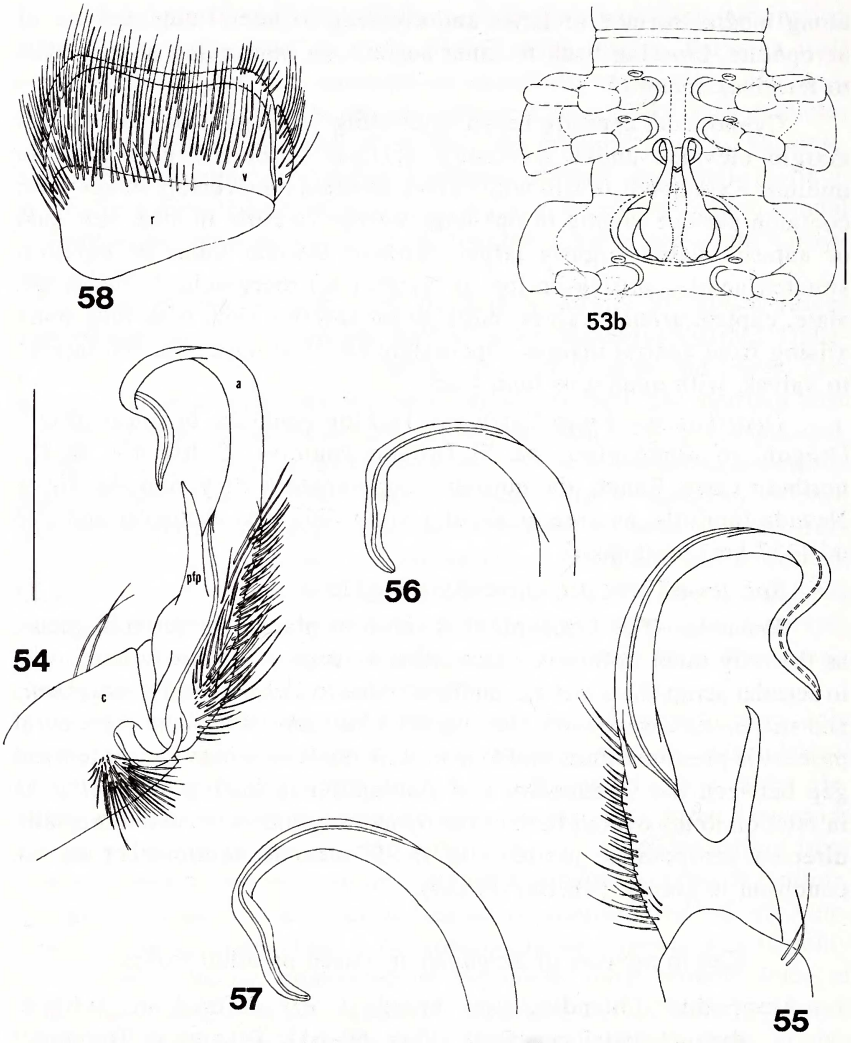
Key to Species of *Selenocheir*, based on adult males.

1. Acropodite subtending very broad, poorly defined arc, without distinct distal curvature (Figs. 60–61); Tehama to Humboldt and Mendocino counties, California ..... *arcuata*, new species

   Acropodite curving definitely downwards or dorsad distally, with relatively distinct distal curve or bend 2

2. Distal part of acropodite, distal to distal curve/bend, variably sinusoid (Figs. 54–57); Shasta to Mendocino and El Dorado counties, California ..... *sinuata*, new species

   Distal part of acropodite without trace of sinusoid pattern (Figs. 65–66); Curry and Jackson counties, Oregon, to Del Norte County, California ..... *directa*, new species



Figs. 53b-58. *Selenocheir sinuata*. 53b, gonopods *in situ*, ventral view of male from El Dorado County, California. 54, left gonopod of holotype, medial view. 55, telopodite of the same, lateral view. 56, distal extremity of acropodite of left gonopod of male from Humboldt County, California, medial view. 57, distal extremity of acropodite of left gonopod of male from W of Burney, Shasta County, California, medial view. 58, left cyphopod of female paratype, caudal view. Abbreviations as in Figures 2-8. Scale line for Figure 53b = 1.00 mm; line for other Figures = 1.33 mm for 54-55, 1.14 mm for 56-57, 1.00 mm for 58.

Selenocheir sinuata, new species

Figs. 53b–58

Hybaphe tersa (nec Cook, 1904): Causey, 1954*a*:222, fig. 1; 1955:91. Chamberlin and Hoffman, 1958 (in part):36. Buckett, 1964:8–9.

Type specimens—Male holotype and 3 male, 7 female, and 3 juvenile paratypes (UCD) collected by J. S. Buckett and M. R. Gardner, 20 December 1966, 2 mi (3.2 km) southwest of Dales, Tehama County, California. One male and one female paratypes deposited at NCSM.

Diagnosis—Acropodite directed generally anteriad from coxa, distal curvature sharp, well defined, distal part variably sinusoid, blade-like throughout length.

Color in Life—Paranota variably red to orange, metaterga black with concolorous red to orange bands along caudal margins or middorsal semilunar blotches.

Holotype—Length 27.6 mm, maximum width 9.5 mm, W/L ratio 34.4%, D/W ratio 33.7%.

Epicranial suture strong, distinct, terminating in interantennal region. Width across genal apices 2.7 mm, interantennal isthmus 1.2 mm. Antennae relatively long and broad, reaching back to midlength of 4th tergite; relative lengths of antennomeres 2>3>6>4>5>1>7; 6th antennomere with microsensilla on outer distal margin. Genae with shallow central impressions. Facial setae as follows: epicranial 2–2, interantennal, subantennal, and frontal not detected and presumed absent, genal 1–1, clypeal about 8–8, labral about 12–12.

Collum broad, ends terminating slightly below those of succeeding tergite. Tergites smooth, polished. Paranota well developed throughout body, broadest on anterior segments, becoming slightly narrower caudad, moderately depressed, continuing slope of dorsum, anterior corners with small but distinct denticle on segments 2–4, broadly rounded on remaining segments, caudolateral corners angular on 2–3, blunt on 4–5, rounded on remaining tergites, becoming progressively angled caudad in caudal half of body. Peritremata moderately distinct, moderately elevated above paranotal surfaces; ozopores located caudal to midlength, opening sublaterad.

Sides of metazonites granular, with distinct, irregularly serrate to jagged ridges subtending coxae through segment 10, becoming progressively indistinct thereafter. Gonapophyses moderately long, apically rounded. Pregonopodal sterna glabrous; 5th sternum with two low, paramedian knobs between 4th legs, much shorter than widths of adjacent coxae, and lower, flattened elevated areas between 5th legs; 6th sternum strongly depressed between both leg pairs to accommodate

curvatures of telopodites. Postgonopodal sterna glabrous, flat, and unmodified, with at most only shallow transverse grooves between leg pairs, caudal margins gently curved. Coxae without projections; prefemora of legs on segments 9-18 with ventrodistal spines, longer and more distinct on segments 11-15; tarsal claws gently curved. Hypoproct broadly rounded, slightly extended in midline; paraprocts with margins strongly thicked.

Gonopodal aperture ovid, without indentations, 1.4-mm wide and 0.7-mm long at midpoint, anterior margin flush with metazonal surface, sides elevating caudad and continuing onto caudal margin, latter flared slightly but not extending caudad. Gonopods *in situ* (Fig. 53b) with acropodites extending forward in parallel arrangement, overhanging anterior margin of aperture, apices curling laterad then mediad. Gonopod structure as follows (Figs. 54–55): Coxae moderate-size, connected by membrane only, without trace of sclerotized sternal remnant; with 2 macrosetae above cannula and dense cluster of a dozen or so setae on protuberance below latter. Prefemur moderately long and broad, with short prefemoral process arising near midlength on anterior side, latter extending to just beyond level of tip of acropodite, broadest basally, sides narrowing and tapering to subacuminate tip on lateral margin, directed toward midpoint of arc of acropodite. Latter arising from prefemur at narrow constriction, relatively long, blade-like for most of length, tapering smoothly and continuously, more so distad, to subacuminate tip, in form of broad open arch, flattened at highest point, curving broadly anteriad at 1/3 length and bent more strongly dorsad at 2/3 length, distal part curving in markedly bisinuate fashion. Prostatic groove arising in pit in prefemur, running along medial surface of latter and crossing to lateral side at base of acropodite returning to inner surface at peak of arch and continuing to terminal opening.

Male Paratypes—In two individuals the acropodites cross *in situ* at the midline instead of lying parallel, and in one male the prefemoral process is shorter in relation to the acropodite.

Female paratype—Length 29.0 mm, maximum width 4.5 mm, W/L ratio 15.5%, D/W ratio 82.2%. Agreeing essentially with males excepting the presence of interantennal, subantennal, and frontal setae, 1-1 each, and paranota more strongly depressed, imparting more vaulted appearance to body. Cyphopod aperture encircling 2nd legs, sides and caudal margin flush with metazonal surface, elevated only midline. Cyphopods *in situ* lying transversely in aperture, common surface visible in opening. Valves (Fig. 58) relatively small, unequal, anterior valve larger, situated nearly entirely on top of receptacle, slightly

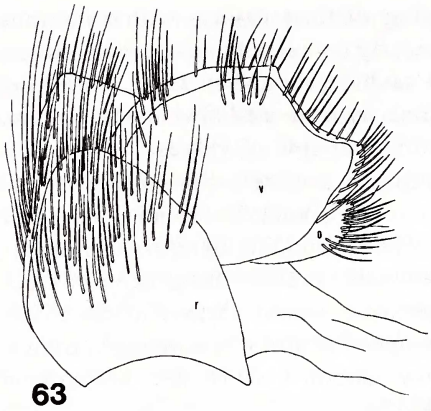
distended mediad but not subtending distinct cavity, with numerous long hairs. Receptacle large, alate, nearly completely enveloping valves, extending halfway up anterior and caudal valvular surfaces, with long hairs arising from ventral margin primarily from medial side. Operculum, moderate-size, closely appressed to lateral side of valves.

Variation—The prefemoral process is noticeably shorter in the male from El Dorado County and rises to a peak in the midline rather than on the outer or lateral margin. The acropodite therefore terminates well above the latter in these individuals, and the distal bend is more gradual, thereby imparting a somewhat sigmoid pattern to the distal curvature rather than sinuate. The sinuate condition is noticeably diminished in males from west of Burney, Shasta County, and Richardson Grove, Humboldt County (Figs. 56–57).

Ecology—The specimens that I collected in El Dorado County were encountered under wet hardwood litter beside a stream in a cove along California highway 49. Those from Shasta County were found under deciduous litter, mostly poison oak, on a bank above the Sacramento River. The male from Butte County was found under a pine log in a pine/fir association near a creek. According to Buckett and Gardner (1968), *S. sinuata*, cited as *Hybaphe* sp., occurs in association with luxuriant vegetation near the bottom of the south wall of the American River Canyon, Placer County, and is thus ecologically segregated from *Wamokia discordis* Buckett and Gardner, which occurs high on the canyon wall, where the slope is steeper, the soil leached, and the vegetation thin.

Distribution—The northern periphery of the Sacramento Valley in Shasta County to the Pacific Ocean in Humboldt County and the foothills of the Sierra Nevada Mountains in El Dorado County, a distance of about 147 mi (236 km) north/south and 154 mi (246 km) east/west. Specimens were examined as follows:

CALIFORNIA: *Shasta Co.*, W of Burney, Moose Camp. Hatchet Cr., M, 3F, 14 May 1966, A. A. Grigarick (UCD); along McCloud R., exact location unknown, 2M, F, 4 May 1929, E. C. Van Dyke (UCD); Project City N of Redding, M, 10 December 1982, B. Miller (SDMNH); Redding, along Sacramento R. trail, 2M, 3F, juv., 28 April 1991, R. M. Shelley (NCSM); 21 mi (33.6 km) W Redding, F, 21 December 1966, J. S. Buckett, M. R. Gardner (UCD); and Inwood, 4 mi (6.4 km) NW Shingletown, F, 20 December 1966, J. S. Buckett, M. R. Gardner (UCD). *Humboldt Co.*, Richardson Grove St. Pk., M, 15 May 1966, H. Wilson (UCD). *Tehama Co.*, 2 mi (3.2 km) S Dales, off CA hwy. 36, 5M, 8F, 3 juvs., 20 December 1966, J. S. Buckett, M. R.



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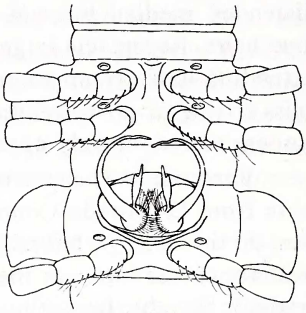

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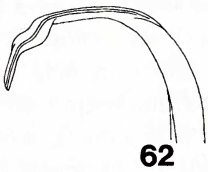

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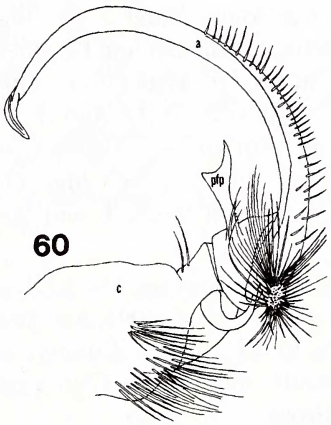

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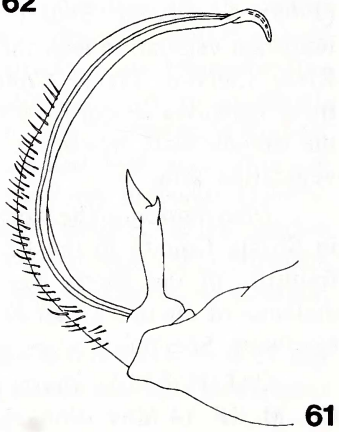

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Figs. 59–63. *Selenocheir arcuata*. 59, gonopods *in situ*, ventral view of paratype. 60, left gonopod of holotype, medial view. 61, the same, lateral view. 62, distal extremity of acropodite of male from 2 mi (3.2 km) N Pashkenta, Tehama County, California, medial view. 63, left cyphopod of female paratype, caudal view. Abbreviations as in Figs. 2-8. Scale line for Fig. 59 = 1.00 mm; line for other Figs. = 1.60 mm for 60-61, 1.33 mm for 62, 1.00 mm for 63.

Gardner (UCD) TYPE LOCALITY; and 22 mi (35.2 km) W Red Bluff, 2M, 3F, 22 December 1966, J. S. Buckett, M. R. Gardner (UCD). *Butte Co.*, Forest Ranch, M, 27 April 1991, R. M. Shelley (NCSM); and Chico, 4M, 3F, 7 May 1968, T. Komo, R. Wilkey, W. Wiard (UCD). *Placer Co.*, 1 mi (1.6 km) E Auburn, 4M, 28 January 1965, M. R., R. C., J. L., B. W., and K. B. Gardner (UCD). *El Dorado Co.*, cove along CA hwy. 49, 1 mi (1.6 km) S Placer Co. line, 4M, juv., 27 April 1991, R. M. Shelley (NCSM); and nr. confluence of North & Middle Forks, American R., M, 26 March 1965, J. S. Buckett, M. R. Gardner (UCD).

The following literature records of *Hybaphe tersa* from Shasta County, in close proximity to each other, are believed to refer to *S. sinuata* and are indicated by the open star in Figure 68. They are the basis for Chamberlin and Hoffman's citation (1958) of Shasta County for *H. tersa* and for Hoffman's citation (1979) of California for *Hybaphe*. The Placer County record is of "an undescribed species of *Hybaphe*" (Buckett and Gardner 1968).

CALIFORNIA: *Shasta Co.*, Mt. Brock (Causey 1954*a*); Low Pass Cr. (Causey 1954*a*, 1955, Buckett 1964); and Madison Cr. (Causey 1955, Buckett 1964). *Placer Co.*, American River Canyon near Auburn (Buckett and Gardner 1968).

Remarks—Buckett and Gardner (1968) also recognized that this species occurs in Shasta and Tehama counties.

Selenocheir arcuata, new species

Figs. 59–63

Type specimens—Male holotype and 9 male and 2 female paratypes (UCD) collected by C. Smith, J. Clover, and F. Ennik, 15 May 1972, at Black Rock Camp along Mill Creek, 18.8 mi (30.0 km) northeast of Red Bluff, Tehama County, California. One male paratype deposited in NCSM.

Diagnosis—Acropodite blade-like basally, becoming subacicular apically, directed anteromediad, subtending broad, poorly defined arc, distal curvature broad, indistinct, distal extremity either uncinate or with short bisinuate section.

Color in life—Unknown.

Holotype—Length 30.8 mm, maximum width 4.8 mm, W/L ratio 15.6%, D/W ratio 68.8%.

Somatic features agreeing with those of *S. sinuata*, with following exceptions:

Width across genal apices 3.2 mm; interantennal isthmus 0.9 mm. Relative lengths of antennomeres 2>3>6>4>5>1>7. Genae with

distinct central impressions. Facial setae as follows: epicranial 2–2, interantennal and subantennal not detected and presumed absent, frontal 1–1, genal 2–2, clypeal about 12–12, labral about 20–20.

Caudolateral corners of paranota angular on segments 2–3, blunt on 4–8, rounded on remaining tergites, becoming progressively angled caudad in caudal half of body.

Sides of metazonites with irregularly serrate ridges subtending coxae through segment 7, becoming progressively indistinct thereafter. 5th sternum with very low, indistinct lobes between 4th legs, flat and unmodified between 5th; 6th sternum with two distinct, widely separated subtriangular lobes subtending anterior (6th) coxae, depressed centrally to accommodate telopodites. Prefemoral spines present on legs on segments 11–18, short and indistinct.

Gonopodal aperture broadly rounded, without indentations, 1.2-mm wide and 0.9-mm long at midpoint, anterior margin flush with metazonal surface, sides elevating strongly caudad and continuing onto caudal margin, latter flared slightly and extending slightly caudad in midline. Gonopods *in situ* (Fig. 59, of paratype) with acropodites leaning laterad then curving broadly anteromediad, tips nearly overlapping, extending well beyond anterior margin of aperture and over 6th sternum. Gonopod structure as follows (Figs. 60-61): Coxae moderate-size, connected by membrane only, with 2 macrosetae above cannula, dense cluster of innumerable setae below cannula, and 4–5 setae above latter cluster. Prefemur moderately long and broad, with short prefemoral process arising anteriad, latter narrow basally, extending distad a short distance, then expanding to shallowly divided tip, medial side longer and more acute. Acropodite arising imperceptibly from prefemur, without constriction, long and narrowly blade-like for most of length, becoming subacicular distad, in form of very broad, open arch, gently curved at highest point, curving broadly anteriad basally and continuing at essentially same curvature to just before tip, where it bends suddenly in uncinate fashion, narrowing thereafter to subacuminate tip. Prostatic groove arising in pit in prefemur, running along medial side of latter and curving onto lateral side of acropodite, angling back onto medial surface at level of base of uncinate curve and continuing to terminal opening.

Male paratypes—The male paratypes agree closely with the holotype except for the prefemoral process, which is slightly different on nearly every individual. Its length and the apical division vary, as the terminations are more unequal than in the holotype. In one paratype,

the lateral termination is absent, and the medial one arises from an otherwise flat surface.

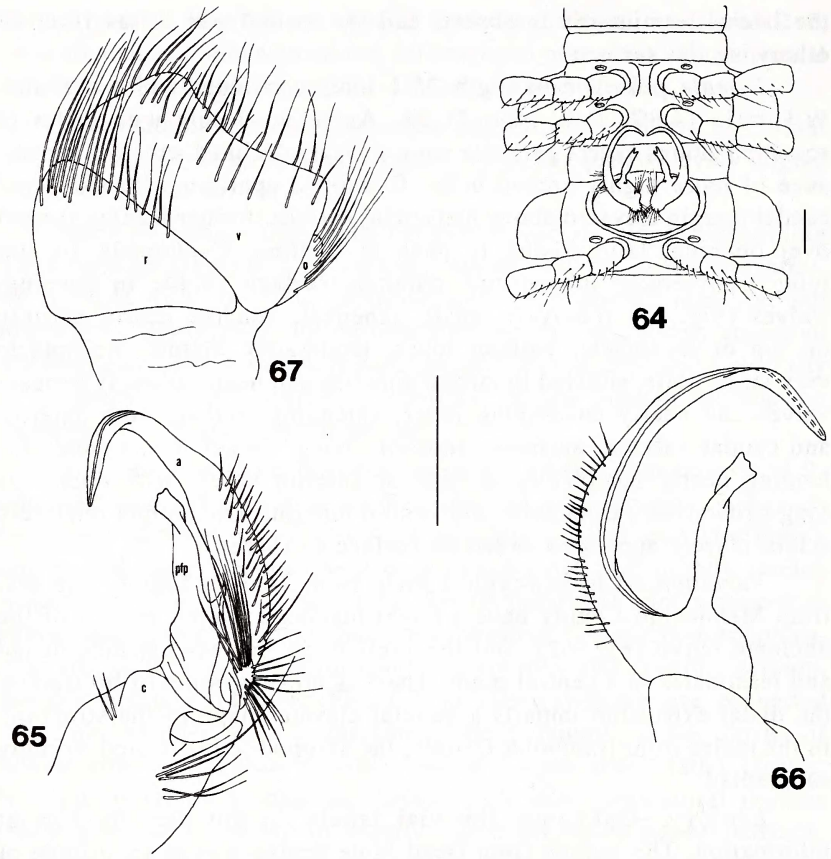
Female paratype—Length 35.1 mm, maximum width 5.2 mm, W/L ratio 14.8%, D/W ratio 71.2%. Agreeing closely with males in somatic features except paranota more strongly declined, creating appearance of more highly arched body. Cyphopod aperture with sides and caudal margin elevated above metazonal surface, former leaning inward over opening, latter rising to peak in midline. Cyphopods *in situ* lying transversely in aperture, common surface visible in opening. Valves (Fig. 63) relatively small, subequal, situated nearly entirely on top of receptacle, without lobes, moderately hirsute. Receptacle very large, alate, situated to medial side but still nearly directly beneath valves and nearly enveloping latter, extending well up both anterior and caudal valvular surfaces, anterior "wing" larger than caudal, extending nearly completely up side of anterior valve, with numerous long hairs arising from sides and ventral margins. Operculum relatively small, closely appressed to lateral surface of valves.

Variation—The non-typical male from Tehama County and that from Mendocino County have a slight bisinuate stretch instead of the uncinate curve (Fig. 62), and the prefemoral process expands distad and terminates in a central point. There is no suggestion of bifuration; the distal expansion imparts a general clavate shape to the structure. In the males from Humboldt County, the acropodite is directed strongly submediad.

Ecology—Unknown; the vial labels do not provide habitat information. The sample from Dead Mule Spring was at an altitude of about 5,150 ft; those from Lake County were collected at 3,910 ft. by ultraviolet light.

Distribution—The northern Sacramento Valley and Coast Range of California, an area of about 84 mi (134 km) east/west and 119 mi (190 km) north/south. Specimens were examined as follows:

CALIFORNIA: *Tehama Co.*, Black Rock Camp along Mill Cr., 18.8 mi (30 km) NE Red Bluff, 10M, 2F, 15 May 1972, C. Smith, J. Clover, F. Ennik (UCD) TYPE LOCALITY; and Dead Mule Spring, along unnamed rd., 2 mi (3.2 km) N Paskenta/Covelo rd., M, F, 29 August 1972, H. B. Leech (CAS). *Mendocino Co.*, 6 mi (7.6 km) N Potter Valley, M, 28 January 1967, J. S. Buckett, M. R. Gardner (UCD). *Humboldt Co.*, 5 mi (8.0 km) N Willow Creek (town), Tish Tang Rec. area, 5M, 21 February 1976, and 2M, 3F, 20 December 1979, A. K. Johnson (NCSM). *Lake Co.*, nr. clear Lake, N side Bartlett



Figs. 64-67. *Selenocheir directa*. 64, gonopods *in situ*, ventral view of paratype. 65, left gonopod of holotype, medial view. 66, telopodite of the same, lateral view. 67, left cyphopod of female paratype, caudal view. Abbreviations as in Figs. 2-8. Scale line for Fig. 64 = 1.00 mm; line for other Figs. = 1.00 mm for 65-66, 0.80 mm for 67.

Mtn. Summit, Mendocino Nat. For., M, F, 28 April 1969, F. Emmik, M. Knudson (UCD).

Selenocheir directa, new species

Figs. 64–67

Type specimens—Male holotype and 20 male, 10 female, and 3 juvenile paratypes (NMNH) collected by A. K. Johnson, 22 December 1977, at Patrick Creek Campground, along US highway 199, 7 mi

(11.2 km) northeast of Gasquet, Del Norte County, California. Seven male and 4 female paratypes deposited in NCSM.

Diagnosis—Acropodite directed strongly submediad, blade-like throughout length, narrowing slightly distad, curving distinctly downward or dorsad distally, without trace of sinusoid curvature.

Color in life—Unknown.

Holotype—Length 24.6 mm, maximum width 3.9 mm, W/L ratio 15.9%, D/W ratio 76.1%.

Somatic features agreeing with those of *S. sinuata*, with following exceptions:

Width across genal apices 2.8 mm; interantennal isthmus 0.9 mm. Relative lengths of antennomeres 2>3>6>4>5>1>7. Facial setae as follows: epicranial 2–2, interantennal 1–1, subantennal 1–1, frontal 1–1, genal 2–2, clypeal about 13–13, labral about 18–18.

Collum terminating at same level as succeeding tergite. Caudolateral corners of paranota angular on segments 2–3, blunt on 4–6, rounded on remaining tergites, becoming progressively angled caudad in caudal half of body.

Sides of metazonites with irregularly serrate ridges subtending coxae through segment 9, becoming progressively indistinct thereafter. 5th sternum with low, rounded elevated areas between 4th legs, slightly depressed between 5th; 6th sternum depressed between both legs to accommodate telopodites. Prefemoral spines present on legs of segments 13–18, short and indistinct.

Gonopodal aperture broadly rounded, without indentations, 1.2-mm wide and 0.6-mm long at midpoint, anterior margin flush with metazonal surface, sides elevating slightly caudad and continuing onto caudal margin, latter extended slightly caudad. Gonopods *in situ* (Fig. 64, of paratype) with acropodites curving broadly submediad, tips nearly overlapping, extending well beyond anterior margin of aperture and overhanging 6th sternum. Gonopod structure as follows (Figs. 65–66): Coxae moderately-large, nearly equal to telopodite in overall bulk, connected by membrane only, with 2 macrosetae above cannula and moderate cluster of setae below. Prefemur relatively short and broad, with moderately long prefemoral process arising anteriad, about half as long as acropodite, broad basally, bent slightly dorsad and twisted at 2/3 length, broad apically. Acropodite arising at slight constriction of prefemur, moderately broad basally, directed submediad, configuration a moderately broad arch, curving broadly at midlength, sides narrowing smoothly and continuously to subacuminate tip. Prostatic groove arising in pit in prefemur, running along medial side of latter

and curving onto lateral margin of acropodite, continuing to terminal opening.

Male paratypes—Except for minor variation in the length, degree of bend, and broadness of the tip, the male paratypes agree with the holotype.

Female paratype—Length, 28.1 mm, maximum width 5.1 mm, W/L ratio 18.1%, D/W ratio 74.5%. Agreeing essentially with males in somatic features except paranota more strongly declined creating appearance of more highly arched body. Cyphopodal aperture very broad, sides and caudal margin elevated above metazonal surface, latter rising to peak in midline. Cyphopods *in situ* lying transversely in aperture, common surface visible in opening. Valves (Fig. 67) moderately large, subequal, without distinct lobes, moderately hirsute, situated nearly entirely on receptacle, nearly completely enveloped by latter. Receptacle large, alate, situated to medial side but nearly directly beneath (dorsal to) valves, extending nearly completely up anterior side of latter, caudal "wing" shorter, with numerous long hairs arising from ventral margin. Operculum relatively large, closely appressed to lateral sides of valves.

Variation—Aside from differences in the length and apical configuration of the prefemoral process, the nontypical males agree closely with the holotype.

Ecology—Unknown.

Distribution—The adjacent corners of southwestern Oregon and northwestern California, an area of about 78 mi (125 km) east/west and 59 mi (94 km) north/south. Specimens were examined as follows:

OREGON: *Curry Co.*, 1 mi (1.6 km) N Gold Beach, on opposite bank of Rogue R., 2M, 30 January 1967, A. Jung (UCD). *Jackson Co.*, Shady Cove, M, 28 March 1972, J. Schuh (FSCA); 10 mi (16 km) E, 6 mi (9.6 km) N Gold Hill, along OR Hwy. 234, M, 22 January 1972, E. M. Benedict (WAS); and 10 mi (16 km) NW Central Point, along OR hwy. 234, M, 22 January 1972, E. M. Benedict (WAS).

CALIFORNIA: *Del Norte Co.*, 7 mi (11.2 km) NE Gasquet, Patrick Cr. Cpgd. along US hwy. 199, 28M, 14F, 3 juvs., 22 December 1977, and 3M, 3F, 21 December 1979, A. K. Johnson (NMNH, NCSM) TYPE LOCALITY.

Remarks—Selenocheir directa bridges the anatomical gaps between the Chonaphini and the Harpaphini, and future workers may conclude that this necessitates synonymizing the tribes. The coxa in *S. directa* is larger in comparison to the telopodal elements than in any of the congeners or any other chonaphines, and the acropodite is directed

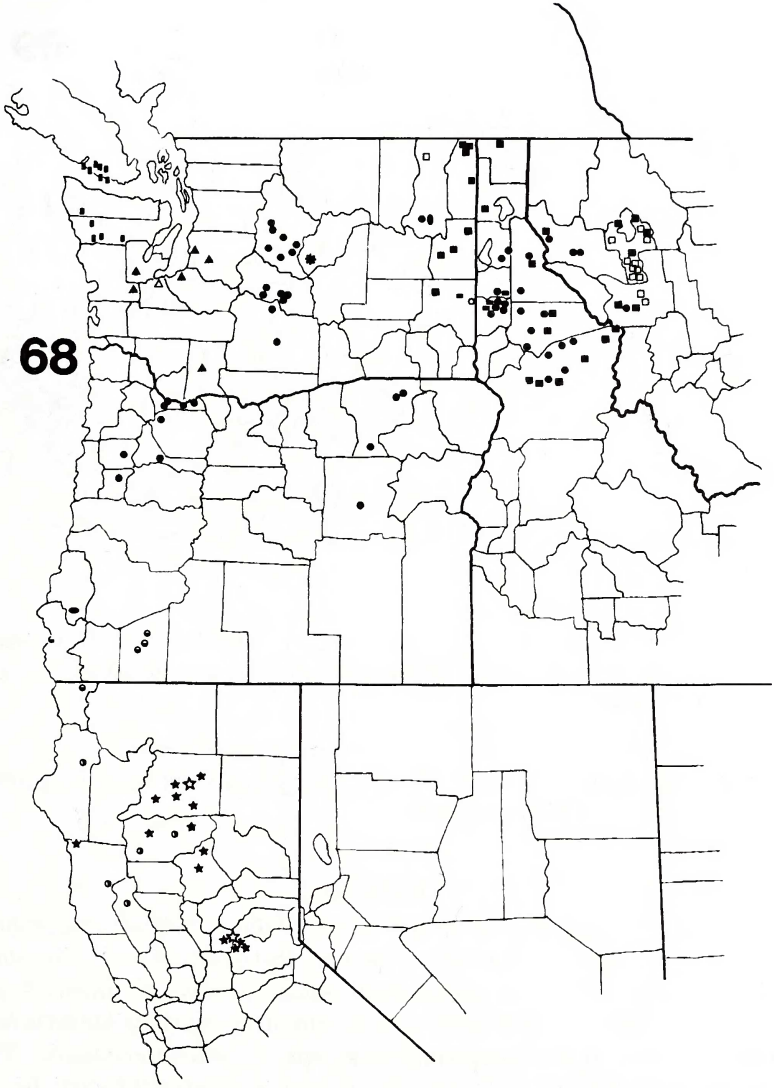


Fig. 68. Distributions of chonaphine genera and species in western North America. dots, *Chonaphe armata*; triangles, *C. remissa*; horizontal oval (southwestern Oregon), *C. evexa*; vertical oval (northeastern Washington), *C. schizoterminalis*; squares, *Montaphe elrodi*; asterisk (central Washington), *M. paraphoena*; vertical rectangles, *T. levii*; horizontal rectangles (Idaho), *Metaxycheir prolata*; stars, *Selenocheir sinuata*; vertical half-shaded dots, *S. arcuata*; horizontal half-shaded dots, *S. directa*. Open symbols denote literature records deemed reliable; the larger, open star signifies three literature sites clustered in the same area.

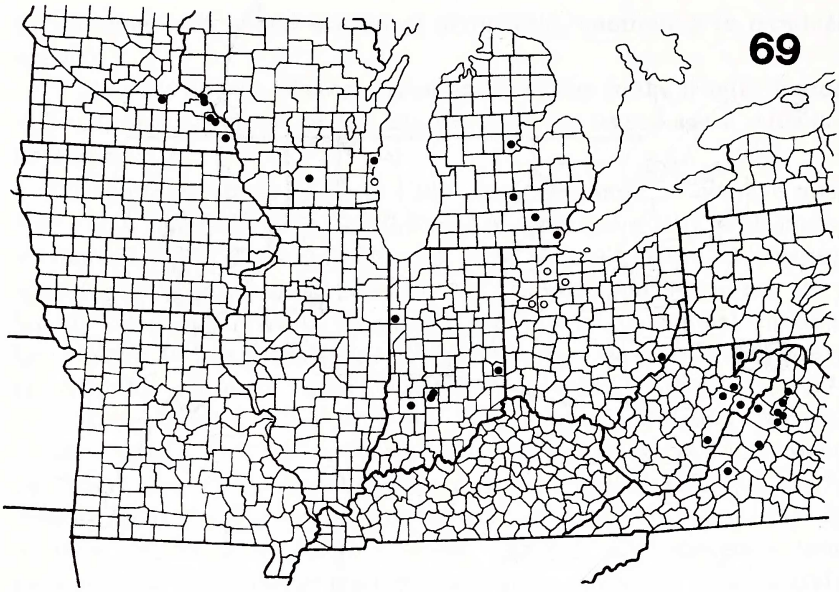


Fig. 69. Distributions of the *Chonaphini*, *Semionellus*, and *S. placidus* in the eastern United States. Open symbols denote literature records considered accurate.

strongly submediad on the coxa. These traits approximate those diagnostic for the Harpaphini (Shelley 1993*d*).

DISTRIBUTION

Species and genera—As shown in Figure 70, the western chonaphine species occupy mutually exclusive ranges, segregated from each other, aside from the region in and around Idaho, where *C. armata* and *Montaphe elrodi* overlap broadly; the former also overlaps *Metaxycheir prolata*, and the latter completely envelops *C. schizoterminalis*. The sympatry in California between *S. sinuata* and *arcuata* may be an artifact because so few records are available from the Coast Range in Lake, Mendocino, Trinity, and Humboldt counties. The northernmost, Humboldt County, population of *S. arcuata* may be allopatric and detached from the rest of the species, which occurs generally to the south-southwest of *S. sinuata*. I have assumed that these populations connect, which accounts for the range overlap with *S. sinuata*; if they do not overlap, *S. arcuata* and *sinuata* are parapatric. Both *S. sinuata* and *Montaphe elrodi* show southward projecting fingers from their

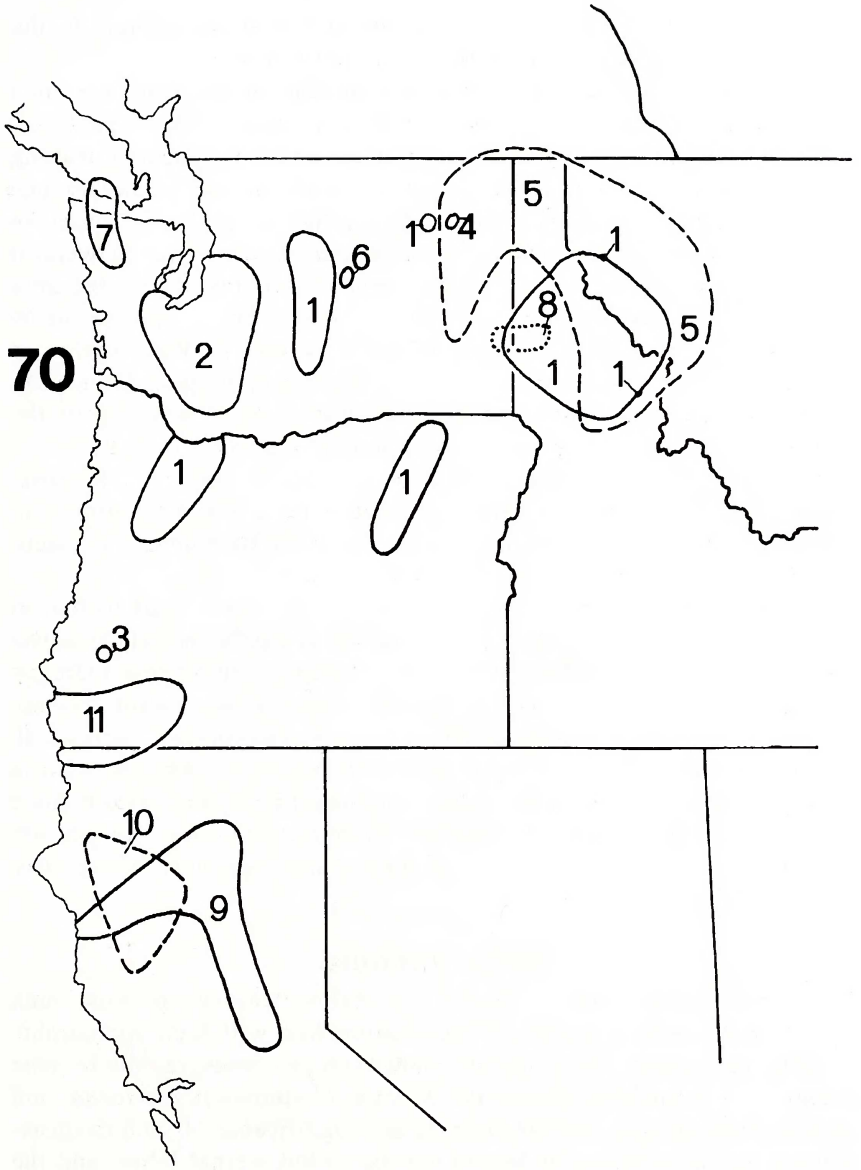


Fig. 70. Comparative distributions of chonaphine species in western North America. **1**, *C. armata*; **2**, *C. remissa*; **3**, *C. evexa*; **4** *C. schizoterminalis*; **5**, *Montaphe elrodi*; **6**, *M. paraphoena*; **7**, *T. levii*; **8**, *Metaxycheir prolata*; **9**, *S. sinuata*; **10**, *S. arcuata;* **11**, *S. directa.*

main ranges; the former is thus the southernmost chonaphine in the West, and the latter, the northern- and eastern-most.

Chonaphe armata and *S. placidus* are the species with the most interesting distributions; they occur in five and four areas, respectively (Figs. 68, 69). In both cases, an ancestral range has fragmented, leaving allopatric populations that have undergone little anatomical divergence and are hence conspecific. Additionally, the distances between the five populations of *C. armata* are much greater than those between it and *C. remissa*, which is effectively parapatric, being segregated only by the Columbia River and the spine of the Cascade Mountains. *Chonaphe remissa* replaces *C. armata* west of the Cascades in Washington, as the latter occurs only on their eastern slope, but in Oregon, *C. remissa* is absent, and *C. armata* occurs only west of the Cascades, in the lower Willamette Valley and eastern foothills of the Coast Range as far south as Benton County. *Chonaphe evexa* is thus an allopatric, southern species, detached from the main generic range by some 125 mi (200 km); *C. schizoterminalis*, in northeastern Washington, is essentially parapatric with a population of *C. armata*.

The picture at the generic level (Fig. 71) is identical to that at the specific, with the exception of *Selenocheir* in California and *Chonaphe* in Washington. *Selenocheir* covers a broad area in southwestern Oregon and northern California with a finger extending southward through the Sierra Nevada foothills. In *Chonaphe*, the ranges of *C. armata* in western Washington and Oregon join with that of *C. remissa* to form a large area with a finger extending southward down the eastern slope of the Coast Range and the western Willamette Valley. Ranges are also mutually exclusive except in Idaho and environs, where they overlap as in the species.

RELATIONSHIPS

Tribal—What seemed to be a straightforward study from such specialized genera as *Chonaphe* and *Semionellus*, with their apomorphic acicular acropodites and elaborate prefemoral processes, rapidly became complex as I pondered forms like *T. levii*, *Montaphe paraphoena*, and *Metaxycheir prolata*, and the meaning and significance of such inconsistencies as the presence of lateral versus medial sternal lobes, and the presence or absence of a sternum. Because the acropodites of its species are as narrowly blade-like or acicular as those of *T. levii* and *M. prolata*, the question arose as to whether *Selenocheir* is also a chonaphine, but with a short, instead of a long, prefemoral process. No other established tribe can accommodate *Selenocheir*, and a monobasic category would be undefinable, so I place it in the Chonaphini. *Selenocheir*

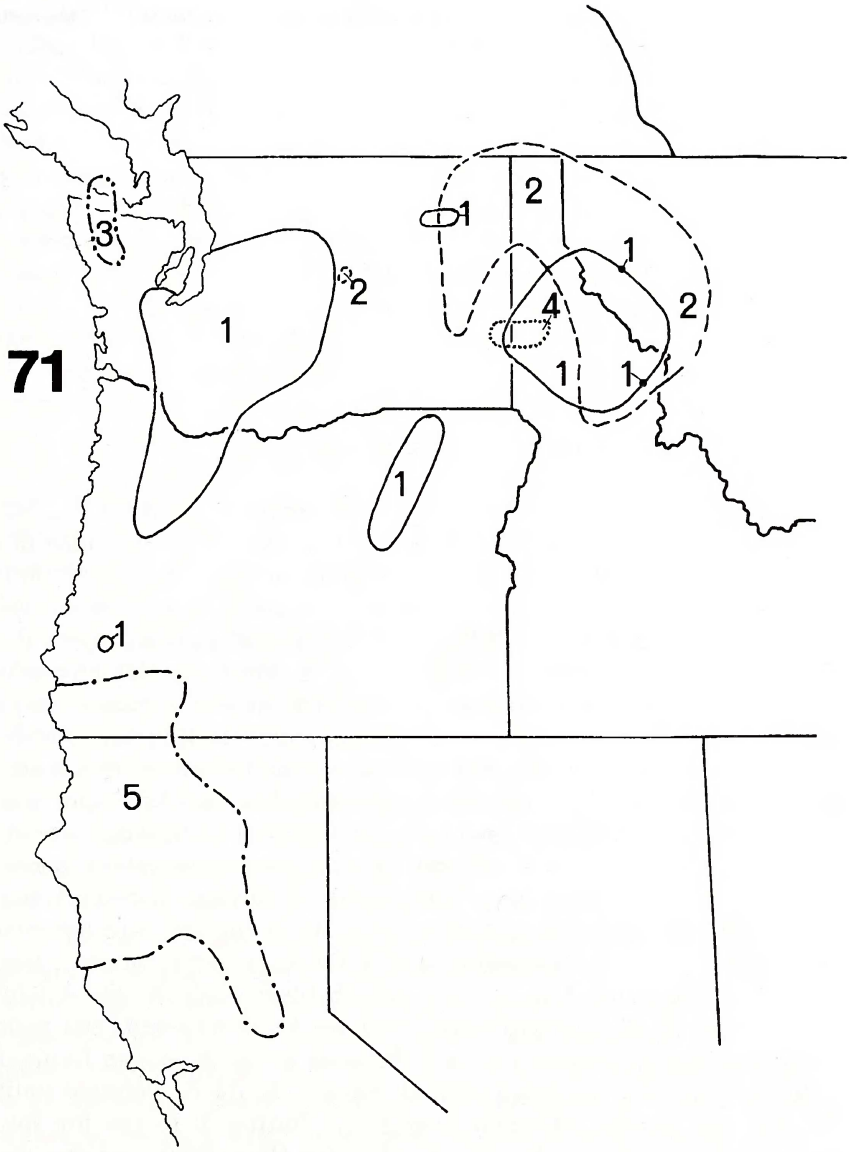


Fig. 71. Comparative distributions of chonaphine genera in western North America. 1, *Chonaphe*; 2, *Montaphe*; 3, *Tubaphe*; 4, *Metaxycheir*; 5, *Selenocheir*.

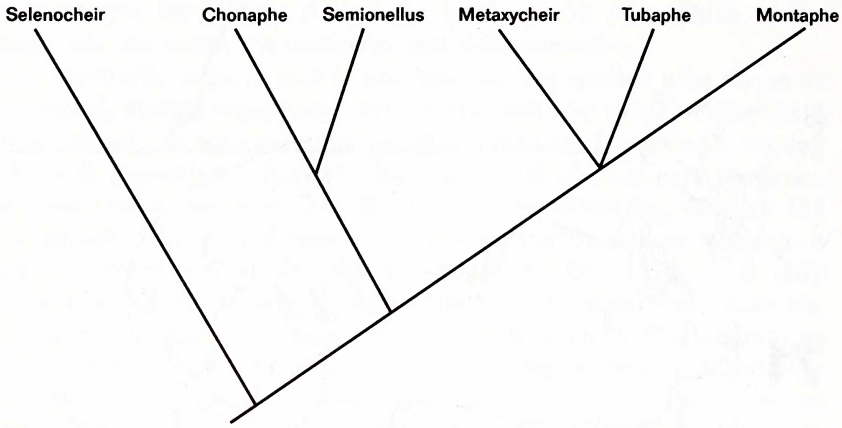


Figure 72. Relationships in the Chonaphini.

sinuata was previously misidentified as *Isaphe tersa* (Cook), a member of the Harpaphini (Causey 1955, Buckett 1964), because of key similarities between *Selenocheir*, particularly *S. directa*, and *Isaphe* (= *Hybaphe*). In *I. tersa*, as in all harpaphines, the coxa is larger than the telopodal elements in overall bulk, and the latter is oriented transversely on the prefemur so as to project directly mediad; the telopodal elements therefore extend directly toward the viewer in medial aspect, so as to provide a head-on perspective rather than a profile (Shelley 1993*d*). In *S. directa*, the coxa is proportionately the largest in the genus, being only slightly smaller than the telopodite, and the telopodal elements are directed anteromediad, or about midway between a head-on view, as in the Harpaphini, and a profile, as in chonaphine genera like *Tubaphe* and *Montaphe*. Consequently, *S. directa*, and to a lesser extent the entire genus *Selenocheir*, span the anatomical gaps between the Chonaphini and Harpaphini, and if future workers conclude that they should be merged, the former name holds priority. As the Asiatic representatives of the Harpaphini have not been reviewed, and their characteristics are poorly known in contrast to the American forms, I believe a decision on this potential merger should be deferred until the Oriental genera are better understood. Suffice it to say for now that the Chonaphini is closely related to the Harpaphini, and that the component taxa of both groups demonstrate a broad range of expressions of a suite of anatomical features.

Generic and Specific—Two obvious chonaphine lineages are apparent—one with expanded, laminate prefemoral processes and acicular acropodites (*Chonaphe* + *Semionellus*), and one in which the prefemoral process is narrow and blade-like, and the acropodite broader and less

acicular (*Montaphe* + *Tubaphe* + *Metaxycheir*). *Selenocheir*, with its short, plesiomorphic prefemoral process, represents a separate, sister line. There are no intermediate forms with partly expanded prefemoral processes or ones of intermediate lengths, an anatomical gap that suggests age and the extinction of intermediate forms. Age is also indicated by the substantial geographical gaps—between intraspecific populations of both *S. placidus* and *C. armata*, between species of *Chonaphe*, between *Metaxycheir* and *Tubaphe*, and most especially between the western faunal regions and *Semionellus*. *Chonaphe evexa* and *schizoterminalis* share an angular elevation on the dorsal face of the prefemoral process distal to the shield, this being a low ridge in the former and a laminate flap in the latter, and appear to be peripheral relicts of an early lineage that has been supplanted by the younger branch leading to *C. armata* and *remissa*, which possesses the thicker, distal projection at the location of the ridge. Although evolving more recently, the *C. armata* + *remissa* lineage is old enough to have undergone substantial fragmentation, with lacunae between the populations of *C. armata*.

Regarding the forms with narrow, blade-like prefemoral processes, the restricted distributions of *Metaxycheir prolata* and *T. levii* also suggest age, and the former in particular seems to hold relict status because it is known only from 4 samples and 6 adults despite inhabiting the most heavily sampled area of Idaho. *Montaphe elrodi*, occupying a broad, cohesive area in the western interior, evolved more recently, and *M. paraphoena*, an enigmatic species, is a possible relict from an intermediate line between the narrow, blade-like and expanded, laminate forms. I am unable to resolve the relationships between these genera and show an unresolved trichotomy in Figure 72.

My overall impression of the Chonaphini is thus one of age. The geographical and anatomical lacunae contrast markedly with the situations in the Eastern and Meso-American tribes Apheloriini, Nanariini, Pachydesmini, and Rhysodesmini, which lack such gaps and evolved more recently (Shelley and Whitehead 1986). The Chonaphini appears to be the second oldest xystodesmid assemblage next to the Orophini, which has an even larger geographical hiatus between its only nearctic representative, *Orophe*, in Idaho and Montana, and the only other known genera *Pamelaphe* and *Kiulinga*, in China (Hoffman 1964, Shelley 1993*e*). Perhaps the Xystodesmidae, or more properly the subfamily Xystodesminae, experimented at an early age with long, twisted gonopodal telopodites and ones with long, slender, comparatively simple acropodites and complex prefemoral processes, before settling

on the pattern of complex, elaborate acropodites and relatively short, simple prefemoral processes. The descendants of such early experimentations survive today in discontinuous ranges as the tribes Orophini and Chonaphini, respectively.

ACKNOWLEDGEMENTS—Field work for this study was supported by grant number 4495-91 from the National Geographic Society; anatomical examinations took place in January 1992, while I was working at the NMNH on a Mid-Career Fellowship from the National Science Foundation. Access to the types of *C. cygneia*, *michigana*, *patriotica*, and *serratus* (holotype), *Leptodesmus borealis* and *L.* (*C.*) *elrodi*, and nontypical material at the NMNH, was courtesy of J. A. Coddington; the type of *T. levii* and nontypical material at the AMNH were loaned by N. I. Platnick; the holotype of *Metaxycheir prolata* (UCD) was donated by L. S. Kimsey; paratypes of *C. serratus* and other samples at the FSCA were provided by G. B. Edwards; and syntypes of *Polydesmus armatus* (PMNH) were loaned by C. L. Remington and R. J. Pupedis. Samples from the following collections were provided by the indicated curators and collection managers: BYU, R. W. Baumann; CAS, W. J. Pulawski; CMN, P. F. Frank and J. A. Fournier; EIL, R. C. Funk; FMNH, D. A. Summers; MCZ, H. W. Levi; MPM, J. P. Jass; RBCM, R. A. Cannings; ROM. D. C. Darling; SDMNH, D. K. Faulkner; TMM, J. R. Reddell; UBC, S. G. Cannings; UCD, the late R. O. Schuster; UMN, R. Hozenthal; UWBM, R. Crawford; UWY, S. R. Shaw; VMNH, R. L. Hoffman; WSU, R. S. Zack; and WU, D. R. Breakey. My colleague W. A. Shear provided valuable samples from his personal collection, and R. Crawford (UWBM) suggested the name, *paraphoena*, for the new species of *Montaphe*. Figures 2–67 were prepared by R. G. Kuhler, NCSM scientific illustrator; Cathy Wood graciously handled repeated word processing chores.

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Received 19 May 1993
Accepted 17 February 1994